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Rust fungi of Austria 1 (excluding *Puccinia* s.l. and *Uromyces*): Melampsoraceae and related families, Gymnosporangiaceae, Ochropsoraceae, Phragmidiaceae, Tranzscheliaceae, and Genera incertae sedis

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Abstract

This first part of an in-depth treatment of Austrian rust fungi (Pucciniales, formerly Uredinales) contains all genera except *Puccinia* s.l. and *Uromyces*. The rust species included here belong to the families Coleosporiaceae, Melampsoraceae, Milesinaceae, Pucciniastraceae (all four in suborder Melampsorineae), as well as Gymnosporangiaceae, Ochropsoraceae, Phragmidiaceae, Tranzscheliaceae, and some taxa of uncertain position.

The introductory part consists of four chapters. Instead of a glossary, a short 'Introduction to the rust fungi' and their terminology is presented. It is based on the life cycle of a well-known textbook fungus, the host alternating *Puccinia graminis*. In the chapter '**Spore states and life cycles of rust fungi**' persisting difficulties of rust terminology are pointed out, followed by detailed overviews of rust sori and spores (especially of aecia and uredinia) and of the diverse life cycles of rust fungi. Two tables summarise the basic modifications of the life cycle and the terms for rust sori and spore types. A brief chapter on rust nomenclature deals mainly with the consequences of the changes in Article 59 of the 'International Code of Nomenclature for Algae, Fungi, and Plants' of 2012 (Melbourne Code) for the scientific names of rust fungi. At the end of the introductory part, the arrangement of rust taxa in the book and abbreviations are explained. A list of the short determination keys completes the introductory chapters.

The main part ('**Rust taxa: rust-host combinations, diagnoses, illustrations, remarks and keys**') is divided into two sections: 'Melampsoraceae and related families' includes the four families of suborder Melampsorineae, followed by 'Other families and Genera incertae sedis'. According to the corresponding introductory chapter, J.C. Arthur's terms for rust sori and spores are adopted in the sense of D.B.O. Savile. The circumscriptions of families and genera in this volume largely agree with those accepted by Aime et al. (2018a) and Aime and McTaggart (2020). Full descriptions or diagnoses of families and genera are not given consistently, but in some cases morphological, taxonomic and nomenclatural issues are discussed in detail. The nomenclature of species mainly follows MycoBank (2024) and/or Index Fungorum (2024), and the checklist in Thiel et al. (2023). The species concept is still more or less in line with the views expressed in E. Gäumann's 'Die Rostpilze Mitteleuropas' (1959) which has also been the taxonomic basis of the second edition of the checklist of Austrian rust fungi by Poelt and Zwetko (1997). This checklist is also the mycofloristic basis of the present volume because a fully updated account of the rust flora of Austria (including recent publications) has been postponed and scheduled for the pending second volume. The main part lists European rust taxa (except *Puccinia* s.l. and *Uromyces*) recorded on host plants occurring in Austria until 1997, and the preliminary, partial '**Alphabetical host-parasite index**' (Appendix 1) lists the European rust hosts occurring in Austria; some of this information is based on inoculation experiments cited in classic rust florae (especially those by Gäumann and Klebahn, see below).

Melampsoraceae and related families (suborder Melampsorineae). In accordance with recent molecular genetic evidence, the Coleosporiaceae are treated in a wider sense, including *Chrysomyxa*, *Coleosporium*, *Cronartium*, *Rossmanomyces* (recently separated from *Chrysomyxa*), and *Thekopsora* (recently transferred from Pucciniastraceae). The Melampsoraceae s.str. contain only the difficult genus *Melampsora*. The species concept adopted for this genus mainly follows two classic works, H. Klebahn's rust volume in 'Kryptogamenflora der Mark Brandenburg' of 1914 and E. Gäumann's 'Die Rostpilze Mitteleuropas' of 1959; infraspecific 'formae speciales' are discussed in several cases. The Milesinaceae include the fern rust genera *Milesina* and *Uredinopsis*, but also *Naohidemyces vaccinii* (recently transferred from Pucciniastraceae) with *Vaccinium* spp. as uredinial hosts. The generic concept within the Pucciniastraceae is far from settled, and the genera *Calyptospora* and *Melampsorella* are still accepted although they

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might be included with *Pucciniastrum* in the future; *Hyalopsora* and *Melampsoridium* are well-delimited genera.

Other families and Genera incertae sedis. This section includes a heterogeneous assemblage of the families Phragmidiaceae (*Gymnoconia*, *Kuehneola*, *Phragmidium*, *Trachyspora*, *Triphragmium*, *Xenodochus*), Gymnosporangiaceae (*Gymnosporangium*), Ochropsoraceae (*Ochropsora*), Tranzscheliaceae (*Leucotelium*, *Tranzschelia*), and two more genera which are not assigned to a family here (*Nyssopsora*, *Triphragmiopsis*).

Key Words

rust fungi, Pucciniomycetes, Pucciniales, Uredinales, phytopathogenic fungi, Austria, plant parasites

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Preface 1 and acknowledgements

The history of this book is quite complex, and we are neither able nor intending to depict all phases in detail. But it may be quite illustrative that the first author, the late Dr. Peter Zwetko (1957–2017), had a combination of a colour atlas and Brandenburger's 'Vademecum zum Sammeln parasitischer Pilze' (1963) in mind when he wrote the first drafts about twenty years ago.

This original concept, however, was finally expanded to a manual of Austrian rust fungi, complete with descriptions and numerous illustrations, including SEM photos. The manuscripts in the residue handed over to us also comprise draft treatments of difficult groups of *Puccinia* and *Uromyces*, but at some point it must have become clear that such a rust funga would be too bulky. The manuscript for the first volume (all genera except *Puccinia* s.l. and *Uromyces*) was delivered to the publisher in portions, and the volume was nearly completed when Peter Zwetko died in July 2017. In parallel, two SEM studies on aecia and an essay on species concepts in European florae of rust fungi were drafted, but only one paper was published before 2017 (Zwetko and Blanz 2012, 2018; Blanz and Zwetko 2018).

In spite of his excellent thesis on *Carex* rusts (published in 1993), Zwetko never attempted to start an academic career at the Institute of Botany (University of Graz), so he made a modest living on working contracts provided by the Austrian Academy of Sciences (e.g., Poelt and Zwetko 1997; Zwetko and Blanz 2004) and on various other jobs. However, the former supervisor of Peter Zwetko, Prof. Josef Poelt, had died in 1995, and Zwetko was the only trained expert in rust fungi in Austria ever since. It did not come as a surprise that nobody felt competent to jump in and finalise the first volume of the present manual in due course. Moreover, rapid progress in understanding the phylogeny of rust fungi (e.g., Aime 2006; Aime and McTaggart 2020) – in contrast to countless open questions on species level – can be a paralysing rather than a motivating mixture for colleagues who are neither familiar with difficult genera like *Melampsora* nor with insufficiently documented or rare taxa.

A pending re-organisation of the commissions within the Austrian Academy of Sciences in April 2024 has finally drawn more attention to the fact that the first volume of this rust funga of Austria is still unpublished. Although we are not quite so knowledgeable in this field, we decided to fill the gaps in the original manuscript (mainly the family Coleosporiaceae, the preliminary host-parasite index, and some introductory passages). Families and genera were adapted to the phylogeny of Aime and McTaggart (2020), with very few recent updates. The rest (about 80% of the present text) has been slightly re-edited, but without alteration of Peter Zwetko's basic concepts.

For the present volume, information on occurrence of the rust species in Austria had to be based on the second edition of the rust catalogue (Poelt and Zwetko 1997), again in accordance with the original manuscript. More recent contributions to our knowledge of the rust funga of Austria (partly already included in the landmark book by Klenke and Scholler 2015) will be evaluated in detail for the second part of the present work, in order to provide a comprehensive host-parasite index and up-to-date information on the occurrence of rust fungi in Austria (see Preface 2 below).

The second part of this rust funga will contain the genera *Puccinia* s.l. and *Uromyces*, together with residual pucciniaceous species assigned to the anamorphic form genera *Aecidium* and *Uredo*. Presumably, the paraphyletic genera *Puccinia* and *Uromyces* will have to be treated in the traditional sense (e.g., Cummins and Hiratsuka 2003), in spite of gradually accumulating evidence which will certainly lead to a more natural arrangement in the future.

Acknowledgements

Thanks are mainly due to two leading personalities in Austrian botany who are not with us any more: For many years, Prof. Friedrich Ehrendorfer (1927–2023) and Prof. Josef Poelt (1924–1995) have promoted the projects within the 'Catalogus Florae Austriae' framework supported by the Austrian Academy of Sciences, including the two editions of the rust catalogue (Poelt 1985; Poelt and Zwetko 1997). Continuity was maintained by Prof. Paul Blanz, corresponding member of the Academy, who has done his best to support Peter Zwetko's research from 1995 onwards and cooperated with him until his death (e.g., Zwetko and Blanz 2004, 2012). Helpful advice for the last-minute completion of this 'resuscitated' manuscript of the first volume came from M. Catherine Aime, Ludwig Beenken, Friedemann Klenke, Hermann Voglmayr, and Karin Windsteig. Nearly all scanning electron micrographs were prepared by Paul Blanz, three by Gerhard Bedlan, and one by Stephan Helfer. Habit photographs and close-ups were mainly provided by Paul Blanz, Julia Kruse and Walter Obermayer, and one figure each by Dan Aamlid, Helene Riegler-Hager, Richard Tafner and Waldschutz Schweiz WSL. Several other copyright holders kindly gave their consent to reproduce illustrations from previously published works, for instance, Duncker & Humblot GmbH (Dietel 1928) and 'Schweizerische Vereinigung für Bryologie und Lichenologie'/Bryolich (Fischer 1904). Special thanks are due to the publishing house Borntraeger-J. Cramer (Stuttgart, www.borntraeger-cramer.de) for permission to use numerous line drawings by Heinrich Klebahn from the rust volume of 'Kryptogamenflora der Mark Brandenburg' (Klebahn 1914).

We hope that the second part of this rust funga can be tackled in due course, preferably by some forthcoming Austrian uredinologist.

Graz and Vienna, 31 January 2024

Christian Scheuer
Irmgard Krisai-Greilhuber

Preface 2

Three issues of the 'Catalogus Florae Austriae' are dealing with rust fungi (Pucciniales, formerly Uredinales) and describe the hitherto known and documented occurrence and distribution of taxa in Austria. The first edition by Poelt (1985) drew attention to enormous gaps in our knowledge of this large and important group of biotrophic parasites. After more than ten years of extensive collecting and a Ph.D. thesis on a very insufficiently known group of rust fungi, Poelt and Zwetko (1997) published a second edition, adding 40 taxa new to Austria. A supplement by Zwetko (2000) contained another few species newly recorded for our country.

The Swiss rust flora by Gäumann (1959) served as the taxonomic basis, but numerous more recent publications had to be taken into account. Therefore, identification and revision of our finds turned out rather difficult: a lot of this additional literature is rather scattered, difficult to obtain, and frequently restricted to small groups of taxa. The debated concepts of species delimitation in rust fungi contributed to the difficulties. Like most other parasites, these fungi are poor in morphological characters, but usually confined to certain host plants. Host specific taxa occurring on very different plants and therefore in different plant communities and/or at different altitudes are often hard to identify by morphological traits. Consequently, host-specificity is an important criterion for the delimitation of species and infraspecific taxa, especially in Gäumann's (1959) *opus magnum*, but also in the works of some of his predecessors and contemporaries. In the first edition of the rust catalogue, Poelt (1985) remarked that such narrowly defined species "can be identified only by the host plant and finally only by experimental or molecular methods, due to the lack of distinct morphological characters; therefore, material collected in the field will have to remain unidentified in many cases. This extreme species concept is theoretically convincing, but practically not feasible". North American and North European authors objected strongly to Gäumann's species concept, especially to a negligence of morphological analysis. However, also the broadly defined 'collective species' of American authors remained controversial. "Without any doubt, such a species concept is not applicable for a geographically delimited treatment" (Poelt 1985). For instance, *Puccinia recondita* 'sensu lato' (causing brown rust of rye, wheat, and numerous other cultivated and wild grasses) is a well-known example for a 'lumped' taxon. It contains a variety of experimentally proven host-specific taxa, but also species which can be separated by morphological and/or molecular genetic methods.

For any scientific treatment of rust fungi, morphological diagnoses as well as information on the taxonomic concepts and on host specificity are essential. Only on such a broad basis can the taxa be compared and identified in a satisfactory manner. Unfortunately, a number of important morphological traits are not or only vaguely described in standard literature, e.g., the wall ornaments of aeciospores. Judging by the characters reported by some previous authors (Gäumann 1959; Wilson and Henderson 1966; Cummins 1971), rusts on *Ranunculus* are hardly distinguishable in their aecial stage (Zwetko and Blanz 2012). Savile (1973) examined aeciospore types in *Puccinia* and *Uromyces* species attacking Cyperaceae, Juncaceae and Poaceae. He criticised that "for most species the usual description is a statement of dimensions and wall thickness, with some such indefinite phrase as 'finely verrucose'" (Savile 1973: 225); see also Holm (1964, 1967) and Zwetko and Blanz (2012, 2018). Extensive morphological studies of aeciospores, also from type material, will be required, and even then we can hardly expect that all *Aecidium* species described by earlier authors will be assigned to a particular *Puccinia* or *Uromyces* species.

This rust flora is also still designed for studying rust fungi in the field. Following the 'Vademecum zum Sammeln parasitischer Pilze' by Brandenburger (1963), it was originally intended to give compact information on host range and alternation, but also on the occurrence of rust fungi in Austria. In a first draft, it consisted of two complementary lists, a parasite-host index and a host-parasite index, both in alphabetical order. The former was based on all European rust taxa recorded on host plants occurring in Austria, the latter on all European rust hosts occurring in Austria. This basic intention and structure were maintained when we decided to upgrade the work with diagnoses, keys, and illustrations. In spite of its volume, the flora can still be used as a 'Vademecum'. Although the flora explicitly relates to Austria, it can also be used for the whole of Central Europe and, with some restrictions, for N and W Europe. The host-parasite index is mainly based on the literature. The larger European herbaria could not be evaluated, except for GZU, W, WU, M, and some records documented in ZT. There are still considerable gaps in our knowledge of rust fungi occurring on wild plants in Europe, both in their taxonomy and geographical distribution (Helfer et al. 2011).

Many rust fungi are narrowly specialised and grow only on one or very few host species. Therefore, an approach to the most probable identification result is already possible in the field, starting with the host-parasite index. Of course this can never replace an identification under the microscope. Therefore, in a second step, we provided the parasite-host index with descriptions referring to all diagnostic microscopic characters, as well as short taxonomic discussions and references to recent studies. In general, long keys to all relevant species of a rust genus are usually not user-friendly, therefore we give only short keys to rust taxa occurring on one plant species or on a group of closely related host plants. The identification process can also start with these short keys.

To enable easy recognition of rust fungi in the field, also habit photographs are provided. Microphotographs of rust spores taken in transmitted light are usually avoided, instead we prefer to present the excellent drawings from earlier masterpieces, mainly Klebahn (1914) and Dietel (1928), in a new arrangement – as well as SEM photographs.

Due to the bulk of this rust flora, it will be published in two parts, but it can still be used as a field guide. The host ranges of the rust taxa treated in the first and in the second part reflect the relationships of their host plants. Rusts on ferns, on conifers and on the families Rosaceae, Ericaceae (incl. Pyrolaceae) and Salicaceae are covered by the first part, rusts on Cyperaceae, Juncaceae, Poaceae, Fabaceae and on other mono- and dicotyledonous families mainly by the second. Thus, the second part will contain only the two genera *Uromyces* (incl. *Schroeteriaster*) and *Puccinia* s.l. (incl. *Cumminsiella*, *Endophyllum*, and *Peristemma*), together with residual pucciniaceous species assigned to the anamorphic form genera *Aecidium* and *Uredo*. In recent years, the genera *Puccinia* and *Uromyces* proved to be paraphyletic, but it is unlikely that the pending nomenclatural changes will soon catch up with the accumulating molecular genetic evidence. Presumably, the two genera will have to be treated in the traditional sense in the second part of this rust flora (e.g., Cummins and Hiratsuka 2003).

The present flora is also designed as a tool for biodiversity and ecology studies in Austrian rust fungi. Altogether 535 rust taxa (496 species, 8 subspecies and 60 varieties) have been counted by Poelt and Zwetko (1997), about 140 further taxa have been expected. Zwetko (2000) after further studies reported 491 definitely documented rust species in Austria. Exactly 3462 plant taxa (Schratt-Ehrendorfer et al. 2022) were recorded from our country. How many of them are known as hosts of rust fungi in Europe? How many host-parasite combinations are recorded from Austria, so far? How many different combinations are possible? Already Poeverlein (1937) noticed that the distribution of rust fungi differs significantly from the distribution of their host plants and he presented an early comparative geobotanical study on the occurrence and abundance of rust fungi in Central Europe. He listed all rust species recorded only locally or not at all, in spite of their common and widespread host plants. Poelt and Zwetko (1997) also pointed out several interesting examples of this sort, e.g., the different distribution patterns of the microcyclic *Uromyces alpestris* and *U. scutellatus* on *Euphorbia cyparissias*. In order to supply further data and stimuli for investigations of the ecology of rust fungi, it is planned to evaluate Poeverlein's (1937) data for S Germany and adjacent regions as well as subsequent studies (e.g., Brandenburger 1994; Urban and Marková 2009; Jage et al. 2010; Klenke and Scholler 2015, and the series of papers edited by Kruse et al. 2014 and so on) in detail, and to incorporate the results into a comprehensive host-parasite index in the second part of the present flora, with helpful indications of host-parasite combinations in relation to the distribution and abundance of the host species in Austria and adjacent regions.

Graz, 4 November 2016

Peter Zwetko(†)
Paul Blanz

Note: This preface was prepared from a draft and partly translated from German.

Figure 1. Dr. Peter Zwetko on a collecting trip (Reinischkogel, Styria, 19 June 2009; photo by Paul Blanz).

Preliminary list of publications by Dr. Peter Zwetko

(*30.01.1957 – †25.07.2017)

Blanz P, Zwetko P(†) (2018) Remarks on species concepts in European Florae of Rust Fungi. In: Blanz P (Ed.) Biodiversity and Ecology of Fungi, Lichens, and Mosses. Kerner von Marilaun Workshop 2015 in memory of Josef Poelt. Biosystematics and Ecology Series 34. Verlag der Österreichischen Akademie der Wissenschaften, Wien, 271–287.

Poelt J, Zwetko P (1991) Über einige bemerkenswerte Funde von entweder adventiven oder apophytischen Rostpilzen der Steiermark. Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark 121: 65–72.

Poelt J(†), Zwetko P (1997) Die Rostpilze Österreichs. 2., revidierte und erweiterte Auflage des Catalogus Florae Austriae, III. Teil, Heft 1, Uredinales. Biosystematics and Ecology Series 12, 365 pp. Österreichische Akademie der Wissenschaften, Wien.

Riegler-Hager H, Scheuer C, Zwetko P (2003) Der Erlen-Rost *Melampsoridium hiratsukanum* in Österreich. Wulfenia 10: 135–143.

Scheuer C, Zwetko P, Blanz P (2014) Phytoparasitische Pilze Österreichs - dokumentiert im Herbarium des Instituts für Pflanzenwissenschaften der Universität Graz. In: Landesmuseum Joanneum (Ed.) 16. Treffen der Österreichischen Botanikerinnen und Botaniker, Graz, 25.9.–27.9.2014, Kurzfassungen, p. 76 [Vortrag].

Zwetko P (1993) Rostpilze (Uredinales) auf *Carex* im Ostalpenraum. Ein neues Artenkonzept. Bibliotheca Mycologica 153. J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin-Stuttgart, 222 pp.

Zwetko P (1993) Rostpilze (Uredinales) auf *Carex* im Ostalpenraum - ein neues Artenkonzept. In: Heiselmayer P (Ed.) 7. Österreichisches Botanikertreffen. 10.06.1993–13.06.1993 in Neukirchen am Großvenediger. Kurzfassungen der Vorträge und Poster. Salzburg, p. 68 [Poster].

Zwetko P (1993) Brandpilze in den Sammlungen des OÖ. Landesmuseums in Linz, Oberösterreich (LI). Beiträge zur Naturkunde Oberösterreichs 1: 11–15.

Zwetko P (1993) Rostpilze in den Sammlungen des OÖ. Landesmuseums in Linz, Oberösterreich (LI). Beiträge zur Naturkunde Oberösterreichs 1: 17–24.

Zwetko P (2000) Die Rostpilze Österreichs. Supplement und Wirt-Parasit-Verzeichnis zur 2. Auflage des Catalogus Florae Austriae III. Teil, Heft 1, Uredinales. Biosystematics and Ecology Series 16. Österreichische Akademie der Wissenschaften, Wien, 67 pp.

Zwetko P (2003) Zur Kenntnis der Rost- und Brandpilze Österreichs. In: Scheuer C (Ed.) 29. Mykologische Dreiländertagung, 9.–14. September 2002, Institut für Botanik, Karl-Franzens-Universität Graz, Tagungsbeiträge. Fritschiana (Graz) 42: 77–82.

Zwetko P (2007) Notes on two collections of *Puccinia caricina* s.l. on *Carex hordeistichos* from Austria. Fritschiana (Graz) 58: 35–38.

Zwetko P, Blanz P (2004) Die Brandpilze Österreichs. Doassansiales, Entorrhizales, Entylomatales, Georgefischeriales, Microbotryales, Tilletiales, Urocystales, Ustilaginales. Catalogus Florae Austriae III/3. Biosystematics and Ecology Series 21. Österreichische Akademie der Wissenschaften, Wien, 240 pp.

Zwetko P, Blanz P (2012) Aktuelle Bearbeitung der Rostpilze Österreichs. Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck (Ed.): 15. Treffen der Österreichischen Botanikerinnen und Botaniker, Innsbruck, 27.9.–29.9.2012, p. 100.

Zwetko P, Blanz P (2012) Aeciospore types in rusts on *Ranunculus* and allied genera. In: Pfosser M, Blanz P (Red.) Pilze - Fungi [Ausstellung im Biologiezentrum der Oberösterreichischen Landesmuseen, 30. März 2012–4. November 2012]. Stapfia 96. Land Oberösterreich, Linz, 105–121.

Zwetko P, Blanz P (2014) Aeciosporen bei Rostpilzen auf Koniferen. In: Landesmuseum Joanneum (Ed.) 16. Treffen der Österreichischen Botanikerinnen und Botaniker, Graz, 25.9.–27.9.2014, Kurzfassungen, p. 87.

Zwetko P(†), Blanz P (2018) Distinctiveness of aecia and aeciospores on conifers. In: Blanz P (Ed.) Biodiversity and Ecology of Fungi, Lichens, and Mosses. Kerner von Marilaun Workshop 2015 in memory of Josef Poelt. Biosystematics and Ecology Series 34. Verlag der Österreichischen Akademie der Wissenschaften, Wien, 271–287.

Zwetko P, Heftberger M (2000) Klein-Pilze. In: Rottenburg T, Petutschnig W, Wieser C (Fachred.) 2. GEO-Tag der Artenvielfalt - Biodiversität. Sattnitz-Wände/ Guntschacher Au. Artenliste Projekt Kärnten. Amt der Kärntner Landesregierung, Abteilung 20 - Unterabt. Naturschutz, Klagenfurt, p. 16.

Zwetko P, Pfeifhofer HW (1991) Carotinuntersuchungen an Rostpilzsporen. Bedeutung für die Physiologie und Taxonomie. Nova Hedwigia 52: 251–266.

Zwetko P, Poelt J (1989) Über einige Rostpilze von den Salzwiesen des Seewinkels (Burgenland, Österreich). Sydowia 41: 367–377.

Zwetko P, Denchev CM, Blanz P (2004) A note on rust and smut fungi on *Carex curvula*. In: Agerer R, Piepenbring M, Blanz P (Eds) Frontiers in Basidiomycote Mycology. IHW-Verlag, Eching, 179–184.

Beside his own publications, Peter Zwetko also contributed numerous identifications and annotations to the schedae of exsiccatae and duplicate series published and distributed by the Institute of Botany (Institute of Plant Sciences) of the University of Graz (Plantae Graecenses, Mycotheca Graecensis, Dupla Fungorum, Dupla Graecensia Fungorum).

Introduction to the rust fungi

The rust fungi form a single order named Pucciniales (formerly Uredinales) of a very diverse subphylum of the Basidiomycota, the Pucciniomycotina. A conservative estimate of the taxonomic diversity of the Pucciniales amounts to 7800 species (Kirk et al. 2008). Rust fungi are obligately biotrophic parasites of vascular plants, i.e., they spend their whole active life on a living host. The interface for their biotrophic parasitism is provided by characteristic haustoria in living host cells. There are many prominent species of economic importance parasitising cultivated plants, for instance the causal agent of black stem rust of wheat and other grasses, *Puccinia graminis*, the coffee rust, *Hemileia vastatrix*, or blister rusts of pines like *Cronartium ribicola*. Obviously such biotrophic parasites undergo a narrow co-evolution with their host plants, which is impressively reflected by the gross host ranges of host alternating genera: gymnosperms/ferns, gymnosperms/angiosperms, angiosperms/angiosperms.

The basic terms and a typical life cycle of a **host alternating** (**heteroecious**) rust fungus of temperate regions are explained here by a popular example known from many textbooks, ***Puccinia graminis*** (Fig. 2). The diversity of rust life cycles and their impact on morphology and lifestyle are treated in separate chapters below. In *P. graminis*, there are only two mating types usually marked by the symbols + and –. The nuclear cycle of *P. graminis* can be termed as haplo-dikaryotic, and the alternation of generations includes one haploid (monokaryotic) and two dikaryotic generations. This implies the occurrence of generation-specific spores/gametes produced in characteristic sori, in our case: four different types of sori and five types of spores/gametes.

Rust fungi are basidiomycetes, and basidia are meiosporangia (meiosporocysts) where meiosis takes place. Every basidium produces four uninucleate basidiospores which are thrown off actively as so-called ballistospores (e.g., Webster and Weber 2007) and dispersed by air currents.

If a basidiospore of *Puccinia graminis* gets in contact with the (upper) surface of a young ***Berberis*** (barberry) leaf, it can germinate, infect the leaf tissue and colonise a certain area of the leaf by a monokaryotic (haploid) mycelium (the gametothallus); therefore, *Berberis* is often termed 'haplophase host'. Simultaneously, the mycelium forms characteristic structures responsible for sexual reproduction at the upper and lower side of the leaf. The first type of sori, the so-called **spermatogonia** (pycnia) are pear-shaped and usually produced on the upper side, in small groups in circular orange-yellow spots (Fig. 2a). In the cavity of the spermatogonium, tiny 'male' gametes (**spermatia**, pycniospores) are detached from specialised cells and offered to insects and similar vectors in a sweet, nectar-like suspension which is exuded as a spherical drop over the ostiole of the spermatogonium. The spermatogonium and the nectar drop are also equipped with a 'female' counterpart, long and thin **receptive hyphae** (trichogynes, 'flexuous hyphae'). Spermatia of the opposite mating type are transferred to the receptive hyphae by arthropods feeding on the nectar and moving from one group of spermatogonia to the next. When a spermatium fuses with a receptive hypha, the male nucleus is released and travels through the hypha down towards the lower side of the leaf where the female gamocytes proper are waiting as a small, dense layer of so-called **basal cells** of the protoaecium (the very young primordium of the aecium). After dikaryotisation in these basal cells, the protoaecia become **aecia**, the second type of sori, which produce chains of 1-celled dikaryotic spores, the **aeciospores**. These spore chains are protected by a layer of firmly connected chains of sterile aeciospores, the **peridium** (also 'pseudoperidium'). At maturity, the peridium splits ± radially and breaks through the lower surface of the leaf, releasing the aeciospores which are dispersed by air currents. In *Puccinia graminis*, the peridium is white and the aeciospores bright orange (Fig. 2b).

Puccinia graminis is a **host alternating** rust fungus, which means that the aeciospores cannot infect further *Berberis* plants. Instead, the aeciospores have to infect the alternate host, a member of the grass family **Poaceae** (e.g., *Triticum aestivum*, wheat), usually through the stomata. The parasite forms a fast-growing dikaryotic mycelium (the sporothallus) in the grass culms and leaves and starts to produce the third type of sori, the **uredinia** (Fig. 2c) which break through the epidermis at maturity and release enormous quantities of rust-coloured, 1-celled, dikaryotic **urediniospores** which will infect further grass plants, providing for highly efficient mass reproduction and dispersal. In contrast to the aeciospores, urediniospores are not formed in chains but singly on pedicels. Towards the end of the growing season, the uredinia are gradually replaced by the fourth type of sori, the **telia** (Fig. 2d) which produce blackish-brown, thick-walled **teliospores** (in the genus *Puccinia*, these are always 2-celled). Their pedicels do not break at maturity (in contrast to those of other *Puccinia* species), so the teliospores of *P. graminis* do not serve for dispersal but only as **resting spores**. The telia overwinter as firm cushions of densely packed teliospores on dead grass culms and leaves. Initially the two teliospore cells are dikaryotic (just like the urediniospores), but karyogamy in *P. graminis* usually occurs in autumn. Therefore, the overwintering teliospore of *P. graminis* consists of two diploid zygotes which are also termed 'probasidia' (Fig. 2e).

In spring, when young *Berberis* leaves become available again, the two teliospore cells ('probasidia') germinate (Fig. 2f), each with a slender, thin-walled meiosporocyst, the **basidium** ('metabasidium'). Subsequently, the basidium forms four thin processes (sterigmata) and inserts transverse septa separating the four haploid nuclei. At the tip of each sterigma, an uninucleate basidiospore is formed and forcibly detached as a so-called ballistospore with the help of 'Buller's drop'.

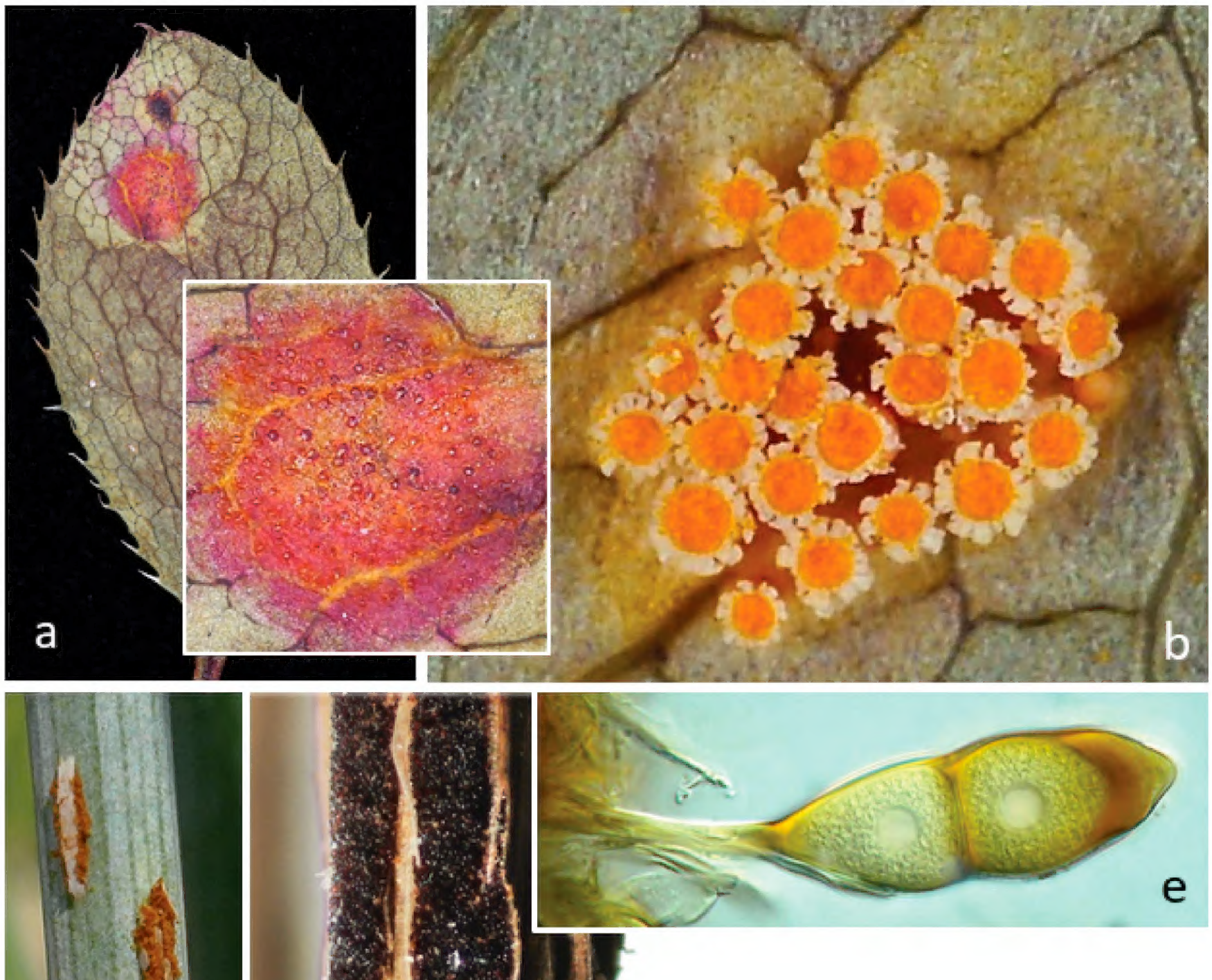


Figure 2. Sori and teliospores of *Puccinia*: **a, b.** *Puccinia graminis* on *Berberis vulgaris*: **a.** Punctiform spermatogonia in conspicuous orange or red leaf spots on the upper side of the leaf; **b.** Cup-shaped aecia with white peridium on the lower side of the leaf, producing orange aeciospores; **c–e.** *Puccinia graminis* on Poaceae: **c.** Uredinia with rust-brown, pulverulent urediniospores on *Secale cereale*; **d.** Culm of *Lolium giganteum* with telia containing densely packed blackish-brown teliospores; **e.** Overwintering 2-celled teliospore with stalk cell and well visible globose nuclear areas in both cells; **f.** *Puccinia moliniae* on *Molinia* (Poaceae); three germinated teliospores with phragmobasidia bearing young basidiospores (arrows) on sterigmata; (**c** by Julia Kruse; **d, e** by Walter Obermayer; **f** edited after Tulasne 1854: pl. 9).

Host terminology: Corresponding with the sori formed at the end of the development on the respective host, *Berberis* is usually named **aecial host**, and the grass is named the **telial host**. The term 'haplophase host' for *Berberis* is not quite correct because a short-lived dikaryotic generation producing aeciospores plus the aecial peridium is inserted after the haploid generation. The haploid generation on *Berberis* ends with the formation of spermatia ('male' gametes) and basal cells ('female' gamocytes) of the protoaecia with receptive hyphae (trichogynes). The short-lived dikaryotic generation on *Berberis* ends with the production of aeciospores. The dikaryotic generation on the grass ends with the production of basidiospores.

Plasmogamy: The type of plasmogamy may vary even within the same species and is certainly not restricted to spermatia and receptive hyphae. Both somatogamy between two compatible monokaryotic hyphae in the host tissue and the Buller phenomenon (when a dikaryotic cell provides the compatible nucleus for another dikaryotisation) may play an important role.

Rust spores: Aecio-, uredinio- and teliospores have more or less conspicuous **germ pores** obviously facilitating spore germination and infection of the host plant (or production of basidia, respectively). **Aeciospores** of *Puccinia* and similar genera are actively discharged by sudden rounding-off of initially compressed spores in the chain, a feature which is apparently absent in more basal rust fungi, e.g., the Melampsorineae (see below). **Urediniospores** are the most uniform spore type within the whole rust fungi. They are always one-celled, with a finely verrucose to spiny wall and well visible germ pores in some groups. **Teliospores** are the most diverse type of spores in the rust fungi, one- to many-celled, well differentiated or hardly recognisable, permanently sessile or breaking off to serve as additional propagules. Thin-walled teliospores do not serve as resting spores and germinate readily.

Life cycle modifications are discussed and explained in more detail below. In Table 1 we summarise the most important and common modifications, based on the life cycle and spore forms of *Puccinia graminis* outlined above. Such a 'complete' developmental cycle (eu-forms) may be prolonged by additional mitotic cycles of reproduction, e.g., secondary (repetitive) aecia or secondary uredinia. But there are also numerous types of 'shortened' life cycles, with or without host alternation. Without any doubt, ecological adaptations of the life cycle and co-evolution with host plants have triggered countless speciation processes, resulting in an exceptional degree of taxonomic diversity. For instance, the short life cycle of a micro-form is certainly of advantage in a short growing season at high altitudes or latitudes, or if the rust fungus grows on a spring geophyte with short-lived aerial parts.

The Russian mycologist V. A. Tranzschel examined related taxa with different life cycles and his conclusions are still quite convincing, at least for the rust fungi of northern temperate regions: (1) The sequence of spore types in the life cycle is invariable (with few exceptions). (2) The place of dikaryotisation is flexible, not restricted to basal cells of aecia, and not depending on plasmogamy between spermatia and receptive hyphae. (3) Karyogamy usually takes place in a teliospore cell (probasidium), meiosis always in the basidium (metabasidium). (4) Autoecious species (especially brachy- and micro-forms) usually grow on the aecial hosts of their heteroecious relatives (Fig. 3); the latter is known as 'Tranzschel's Law' (e.g., Shattock and Preece 2000).

Spore states and life cycles of rust fungi

The terms used in this rust flora are explained in detail below, under the subheadings 'Overview of spore states' and 'Overview of life cycles'. For a quick glance at important terms and their synonyms see Tables 1, 2 (p. 171).

A note on the debated terminology of spore states

N.B.: Only in the present subchapter the terms are given as used by the cited authors. In all other parts we apply a uniform terminology.

"For more than half a century uredinology has suffered from a deficiency, that is the lack of a generally accepted terminology" of the spore states and life cycles (Holm 1984: 221). This situation still persists. The "old European terminology" (l.c. 222) was mainly based on terms already used by De Bary (e.g., 1865, 1866): spermogonia, aecidia, uredosori, teleutosori. De Bary's definition of these spore states is based on both, their position in the life cycles and their morphology. Arthur (1905) introduced a new set of convenient, short terms for the spore states, excluding ambiguous terms identical with generic names like *Aecidium*, *Caeoma*, *Peridermium* and *Uredo*: spermogonium was replaced with pycnium, aecidium/caeoma/peridermium with aecium, uredo/uredosorus with uredinium (later 'uredium'), teleutosorus with telium. Arthur et al. (1907–1924) used these new terms in the 'North American Flora'. Although Arthur united some morphologically different types of sori under the term 'aecium' there, the definition of this spore state was still based on both, the position in the life cycle and the morphology of the respective type of aecium.

Subsequently Arthur wanted to go further, i.e. to establish "terms for the positions in the life cycle that did not have a specific morphologic connotation" (Hennen and Hennen 2000: 123). In the course of these efforts, Arthur (1925, 1932) gave his terms new meanings correlated with the alternation of generations: "Arthur (1925) accepted the concept that spermogonia and aecia are structures produced on the thallus (body) of the gametophyte generation, [and] that aeciospores initiate a new thallus (body) which represents the sporophyte

Table 1. Basic modifications of the life cycle of rust fungi as defined by the presence or absence of aecia, uredinia, telia, and basidia (especially in brachy- and micro-forms spermatogonia are often absent).

	Aecia = I	Uredinia = II	Telia = III	Basidia = IV	Terms for life cycle	Examples (mainly from the present volume)
With host alternation (heteroecious)	**I**	**II**	**III**	**IV**	hetereu-form (macrocyclic)	*Puccinia graminis* *Cronartium flaccidum* *Melampsora allii-populina*
	I	–	**III**	**IV**	heteropsis-form (demicyclic)	*Chrysomyxa rhododendri* (with secondary aecia [= Ib] instead of uredinia on the telial host) *Gymnosporangium sabinae*
Without host alternation (autoecious)	**I**	**II**	**III**	**IV**	auteu-form (macrocyclic)	*Melampsora liniperda* *Phragmidium rubi-idaei*
	I	–	**III**	**IV**	autopsis-form (demicyclic)	*Gymnoconia peckiana* *Trachyspora alchemillae*
	–	**II**	**III**	**IV**	brachy-form (brachycyclic, hemicyclic, 'microcyclic' s.l.)	*Kuehneola uredinis* (with primary + secondary uredinia, IIa + IIb) *Triphragmium ulmariae* (with primary + secondary uredinia, IIa + IIb)
	–	–	**III**	**IV**	micro-form (incl. lepto-form) (microcyclic)	*Tranzschelia anemones* *Chrysomyxa abietis* (lepto-form)
	I	–	–	**IV**	endo-form (endocyclic)	*Endophyllum euphorbiae-sylvaticae*
Without host alternation – insufficiently known?	–	**II**	**III**	**?**	hemi-form (hemicyclic)	?*Thekopsora agrimoniae* ?*Melampsoridium carpini* (in Central Europe)
	I	–	–	–	anamorphic	*Melampsora* sp. (syn. *Caeoma scillae*)
	–	**II**	–	–	anamorphic	*Uredo colchici-autumnalis* *Tranzschelia discolor* (certain strains)

Table 2. Sori of rust fungi, with corresponding spore forms/gametes/basidia in square brackets.

Symbol	Preferred term in the present treatment	Important subterms	Important synonymous terms
0	spermatogonia (sing. spermatogonium) [spermatia]		spermogonia (sing. spermogonium) [spermatia] pycnia (sing. pycnium) [pycniospores]
I	aecia (sing. aecium) [aeciospores]		aecidia sensu lato (sing. aecidium) [aecidiospores] aecidia sensu stricto, aecidioid aecia (anamorphic form genus: *Aecidium*) roestelioid aecidia/aecia (anamorphic form genus: *Roestelia*) caeomata (sing. caeoma), caeomoid aecidia/aecia (anamorphic form genus: *Caeoma* auct.) peridermia (sing. peridermium), peridermioid aecidia/aecia (anamorphic form genus: *Peridermium*)
		Ia primary aecia	aecioid aecia
		Ib secondary aecia	aecioid uredinia
II	uredinia (sing. uredinium) [urediniospores]		uredosori (sing. uredosorus) [uredospores] uredia (sing. uredium) [urediospores] (anamorphic form genus: *Uredo* auct.)
		IIa primary uredinia	uredinioid aecia, uraecia
		IIb secondary uredinia	uredinioid uredinia
		II* amphisporic sori [amphispores, or amphispores with intermixed teliospores]	amphisori, amphioid uredinia
III	telia (sing. telium) [teliospores, incl. lepto-spores (not dormant) and mesospores]		teleutosori (sing. teleutosorus) [teleutospores, probasidia]
		IIIa primary telia	
		IIIb secondary telia	
		III* basidiosori [basidia]	
IV	basidia (sing. basidium) [basidiospores]		promycelia (sing. promycelium) [sporidia] metabasidia [basidiospores]

generation" of plants from the algae, mosses, liverworts, and through all of the groups of vascular plants (Hennen and Hennen 2000: 118–119). In the 'Manual of the Rusts in United States and Canada' Arthur (1934) finally abandoned all 'morphological connotations' he had accepted earlier in the 'North American Flora'. Aeciospores were defined as "non-repeating spores produced as a result of dikaryotisation", urediospores as "repeating vegetative spores produced on a dikaryotic mycelium" (Cummins and Hiratsuka 1983: 2).

Figure 3. An example for Tranzschel's Law: **a.** Aecia (with orange aeciospores) of an *Uromyces* species (*Uromyces pisi* group = *Aecidium euphorbiae* s.l.) on *Euphorbia cyparissias*, a hetereu-form alternating between the *Euphorbia* (aecial host) and Fabaceae (telial host); **b.** Telia (with dark-brown teliospores) of *Uromyces* cf. *alpestris*, one of the related micro-forms on *Euphorbia cyparissias*. – In both cases, infected *Euphorbia* shoots usually do not flower, and their leaves are often distinctly shorter and broader than healthy ones; note the spermatogonia associated with both, aecia and telia; (**a, b** by Walter Obermayer).

These new definitions led to new morphological descriptive terms which were adopted by many American and rejected by most European authors (e.g., Guyot 1938, 1951, 1957; Gäumann 1959; Majewski 1977, 1979) who followed the terminology of De Bary. For instance, 'uredoid aecia' sensu Arthur means that these aecia 'resemble' uredinia (morphologically they are uredinia and usually associated with spermatogonia); 'aecioid uredinia' sensu Arthur means that these uredinia 'resemble' aecia (morphologically they are aecia but not associated with spermatogonia). "The only 'morphology' in Arthur's new system was the nuclear condition of the initiating mycelium: monokaryotic for aecia and dikaryotic for uredinia and telia" (Savile 1988: 387). Such an 'ontogenic' terminology forces us to use different terms for obviously homologous structures.

In the 'Illustrated Genera of Rust Fungi' Cummins (1959) adopted the 'ontogenic' terminology introduced by Arthur (1925, 1932) and implemented in 'The Plant Rusts' (Arthur et al. 1929) and in the 'Manual of the Rusts in United States and Canada'(Arthur 1934). Since then, the terminology of spore states and life cycles of rust fungi has been discussed controversially by several authors, e.g., Gäumann (1964), Laundon (1967, 1972, 1973), Savile (1968, 1979, 1988), Hiratsuka (1973b, 1975), Holm (1973, 1984, 1987), Durrieu (1979), Cummins and Hiratsuka (1983, 2003), Poelt and Zwetko (1997), and Hennen and Hennen (2000). Moreover, some authors of European rust florae were not quite aware of the pitfalls and mixed terms from De Bary's and Arthur's terminology.

In agreement with Savile (1979) we follow De Bary's concept but adopt the following convenient terms for the spore states introduced by Arthur (1905) and used in the 'North American Flora' (Arthur et al. 1907–1924): aecium (incl. aecidium, caeoma, peridermium), uredinium, and telium. The same terminology is applied in the present standard identification handbook by Klenke and Scholler (2015).

Overview of sori and spore states

Jørstad (1964a: 28) noted, that in his "text 'aecidia' is often used as a common term for aecidia and caeomata". His foot-note shows that the old European terminology

is somewhat problematic. Uredinologists used to treat the names of anamorph taxa as synonyms, as soon as the whole life cycle of a rust fungus has been detected, and referred to the name of the teleomorph as species name. This practice lasts for more than hundred years. In Gäumann's (1959) discussions, the terms 'die Uredo', 'die Aecidien', 'die Caeomata' referred to spore states without saying. However, the mixing of generic names like *Aecidium*, *Caeoma* and *Uredo* with names of spore states causes problems and confusion. The name *Uredo* had been used for the uredinial state of the whole rust fungi by many authors for a long time. According to Cummins and Hiratsuka (2003) genera like *Melampsora*, *Ochropsora*, *Puccinia*, *Tranzschelia* and *Uromyces* have uredinia of *Uredo*-type. When including the anamorphs of all these genera, *Uredo* represents a spore state but not a taxon. Nevertheless, the definition given by Cummins and Hiratsuka (2003) for the anamorph genus *Uredo* is much narrower than it is traditionally. Besides *Uredo*, several other anamorph genera apply to the uredinial states of rust fungi, e.g., *Calidion*, *Malupa*, *Milesia*, and *Uredostilbe*. The genus *Calidion* "was established to accommodate the uredinial state of a rust on a fern" (Cummins and Hiratsuka 2003: 37), but also the genus *Phragmidium* (a rust on Rosaceae) has uredinia of the *Calidion*-type. So far, the way of treating anamorphic genera by uredinologists is unsatisfactory. Therefore, a term or name should not be used for both, taxon and spore state. Arthur (1905) has already developed such a terminology of spore states which is applied here in the sense of Savile (1979, see above). For a basic overview of the terms for rust sori and spores see also Table 2 (p. 171).

0: Spermatogonium ('spermogonium', pycnium)

This organ produces spermatia (pycniospores) and nectar, which attracts insects. Production of spermatogonia is one of the most spectacular phenomena in the world of phytoparasitic fungi. Many rusts induce formation of pseudoflowers (Fig. 4) that resemble true flowers in colour and shape (Pfunder and Roy 2000). Usually, spermatogonia are produced on bright yellow, reddish or purple-red leaf spots and swellings, often also on deformed petioles and stems in crowded groups of various size. Like true flowers, fungal pseudoflowers present a sweet-smelling nectar, which contains spermatia that are transferred by nectar-feeding insects (Pfunder et al. 2001). They are thus analogous to the entomophilous perfect flowers.

Figure 4. Pseudoflowers of rust fungi: **a.** *Gymnosporangium* sp. on *Sorbus aucuparia*; like in many other rust fungi, the bright, often circular, reddish or orange leaf spots with crowded spermatogonia serve as pseudoflowers providing nectar; **b.** *Endophyllum euphorbiae-sylvaticae* (Pucciniaceae) on *Euphorbia amygdaloides*, forming a greenish-yellow pseudoflower at the shoot tip; the leaves of the pseudoflower are densely covered with spermatogonia; (**a** by Walter Obermayer; **b** from Poelt and Zwetko 1997: 328).

I: Aecium (aecidium, caeoma, peridermium, etc.)

This sorus bears aeciospores. Usually, these are the first dikaryotic spores in the life cycle. In many rust fungi, they initiate the alternation to another host. Aeciospores are catenulate, i.e., they are produced in chains. Usually, their walls are described as verrucose, but in many instances, however, the understanding of morphological criteria in aeciospore ornamentation is inadequate (Savile 1973; Zwetko and Blanz 2012, 2018).

Aecia are produced on leaves, branches, stems and cones where the fungus often causes bright yellow, reddish or purple-red discolouration and deformation of the surrounding host tissue. In addition, the spores in the aecia are usually bright orange by carotenes and are, therefore, easily visible. But in some genera (e.g., *Milesina* and *Uredinopsis*) and in some *Puccinia* and *Uromyces* species (e.g., *P. phragmitis* and *U. appendiculatus*) the spores are hyaline.

According to their gross morphology, the following main types of aecia are distinguished (these terms are derived from the genera *Aecidium*, *Caeoma*, *Peridermium* and *Roestelia*):

(1) Aecidioid aecia are usually cup-shaped with aeciospores borne within the whitish, cylindric peridium. When mature, their well-developed peridium is regularly opening at the roundish apex, and the revolute margin of the peridium is ± divided into several irregular lobes, which are usually not tapering towards the top. The peridial cells are ± rhomboidal. This type of aecia is characteristic for the *Puccinia-Uromyces* complex and can be found on numerous angiosperms except Poaceae, and (at least in Europe) Juncaceae and Cyperaceae. Usually, aecidioid aecia occur soon after the spermatogonia in spring.

Aeciospores of the *Puccinia-Uromyces* complex (Fig. 5) have characteristic patterns of wall ornamentation. In species on several members of Ranunculaceae and Asteraceae, the apical spore region has been found to exhibit conspicuous features, either a smooth, round cap or a hole, surrounded by an annulus (Zwetko and Blanz 2012). These features are hardly recognisable in a light microscope, and have, therefore, not been described before. However, these features help to recognise apex and basis of isolated aeciospores. When knowing the position of the apex, the regular sequence of spore surface zonation from the apex to the base is evident. It consists of a small, circular, finely verrucose apical zone, surrounded by a broad belt with coarse warts or with coarse warts and dehiscent platelets, respectively. These large platelets have been termed 'abfallende Plättchen' by Klebahn (1914), 'refractive granules' by Holm (1967), or 'pore plugs' by Savile (1973). Shape and size of these platelets provide valuable taxonomic characters (see Holm 1967; Savile 1973; Zwetko 1993). The surface of the basal hemisphere is finely verrucose as it is at the apex. Therefore, the spore surface is not bizonate – as supposed by Savile (1973) – but trizonate.

(2) Aecidioid aecia of the Ranunculaceae-Rosaceae rusts *Ochropsora* (Ochropsoraceae), *Tranzschelia* and *Leucotelium* (Tranzscheliaceae) differ from those of the *Puccinia-Uromyces* complex by their broad revolute peridium, which is divided into a few broad lobes; the lobes are tapering towards the top. The aecia arise from a systemic mycelium, which can persist for years. They cover the lower surface of the leaves ± completely. Infected leaves are paler, the stems are longer, and affected plants usually do not flower. The spores of this type of aecia exhibit an uncommon character. Their walls are pigmented, and their contents lack carotenes. Already Sydow and Sydow (1904) emphasised that the aeciospores of *Puccinia* mostly have a hyaline wall, and the orange-yellow or orange-reddish colour of their spore contents is due to the presence of carotenoid-rich lipid droplets (Zwetko and Pfeifhofer 1991).

(3) Caeomoid aecia in the stricter sense mainly occur in the genus *Melampsora* and lack peridia, but some *Melampsora* species have peridial cells adherent to the epidermis of the host plant. In *Mikronegeria* a single layer of overlying thin-walled cells exists; this layer has little resemblance to a peridium, and breaks up with the overlying host epidermis (Peterson and Oehrens 1978). *Melampsora* and *Mikronegeria* produce aecia on conifers, the former also on some angiosperms.

(4) Caeomoid aecia on Rosaceae are produced by *Phragmidium* and other Phragmidiaceae. In analogy to paragraphs 1, 3, 5 and 6, this type of aecia could better be named **lecytheoid aecia**, after the anamorph taxon *Lecythea* Lév. The aecia on this host family and the ornamentation of their aeciospores distinctly differ from those of *Melampsora* and *Mikronegeria*, they represent a separate type of aecia. Aecia of *Phragmidium* are surrounded by clavate paraphyses. Aecia of *Melampsora* and *Mikronegeria* lack paraphyses.

Sometimes, it is difficult to distinguish aeciospores and urediniospores in this family. The aecio- und urediniospores of *Phragmidium fragariae*, for instance, show the same ornamentation of the spore wall in SEM, i.e. plateau-shaped warts, with small spines on the plateau. Such warts are also known from aeciospores of other *Phragmidium* species, e.g., *Ph. tuberculatum* (Bedlan 1984; Wahyuno et al. 2002). Thus, the urediniospores of *Ph. fragariae* might be secondary aeciospores. On the other hand, there are also *Phragmidium* species with echinulate aeciospores which are very similar to urediniospores, e.g., *Ph. mucronatum* (l.c.). – The aeciospores of the genus *Trachyspora* are interpreted by several authors as urediniospores or 'uredinioid aecidiospores' (e.g., Gäumann 1959; Wilson and Henderson 1966; Gjærum 1974; Helfer 2005; Klenke

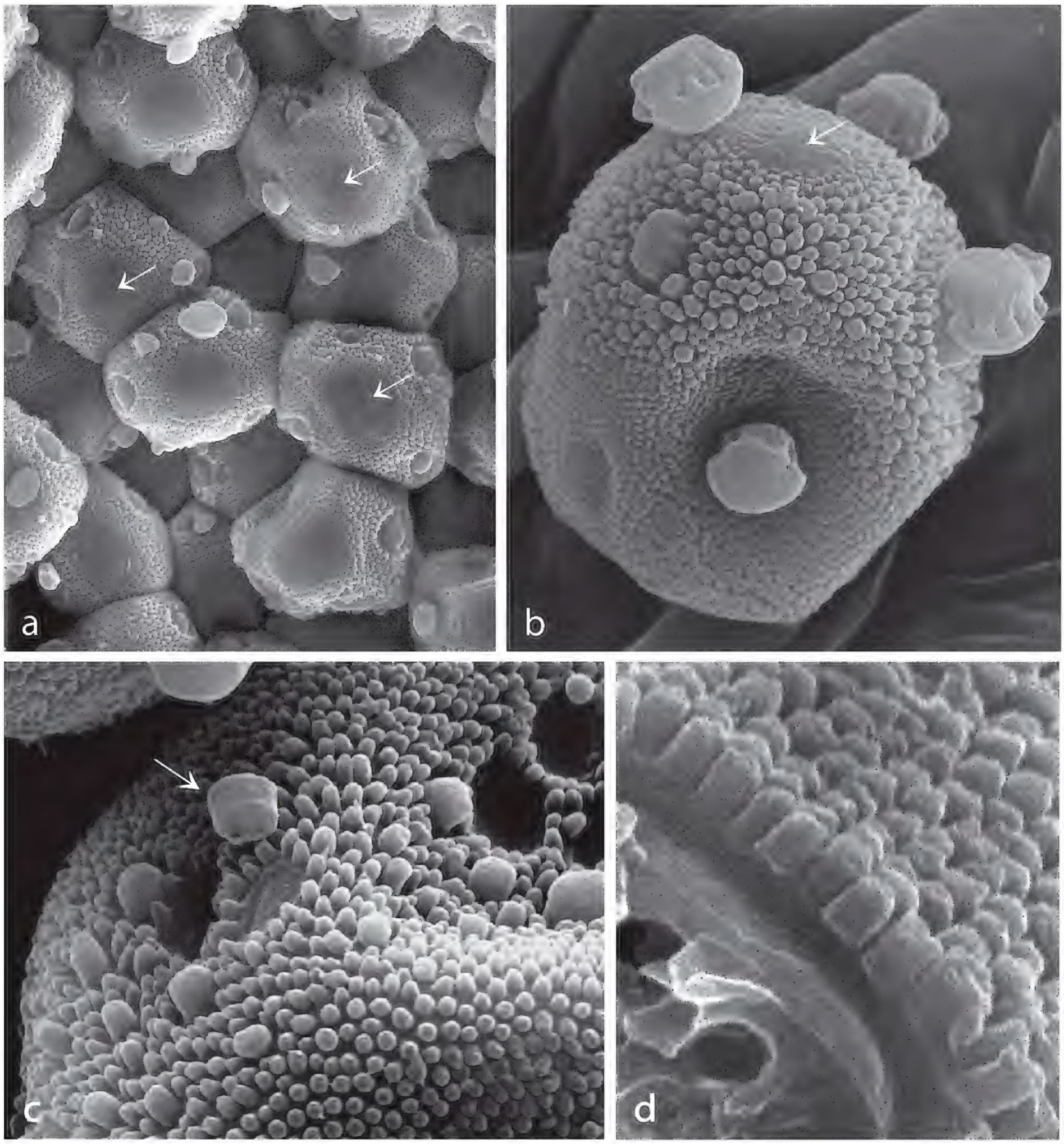


Figure 5. Aeciospores of the *Puccinia-Uromyces* complex: **a.** *Puccinia poae-aposeridis* on *Aposeris foetida*; view into an open aecidioid aecium showing the uppermost spore of each chain with an apical cap (arrows) surrounded by a broad zone of larger warts and a few dehiscent plugs; **b.** *Uromyces alpinus* on *Ranunculus* cf. *montanus*; single aeciospore with a smooth apical cap (arrow) surrounded by a ring of fine warts followed by a belt of larger warts and mostly detached plugs; the basal hemisphere carries uniform fine warts; **c.** *Puccinia bromina* subsp. *symphyti-bromorum* on *Pulmonaria australis*; note the simple smooth warts with rounded tops and the germ pore beside its detached plug (arrow); **d.** *Puccinia recondita* s.l. on *Thalictrum aquilegiifolium*; broken aeciospore wall with similar cylindrical warts in side view; (**a–c** from Zwetko and Blanz 2018: 274, 275, 282; **d** by Paul Blanz).

and Scholler 2015). Henderson (1973) studied the ultrastructure and development of these spores, and the ontogeny of the spine-like surface sculpture confirmed that they are aeciospores.

(5) Peridermioid aecia are cylindrical, tongue-, sac- or blister-shaped. The peridium consists of relatively long and narrow, thick-walled cells arranged in one or several layers. It is irregularly fragmented at maturity. Such aecia are characteristic of the families Coleosporiaceae (incl. Cronartiaceae), Milesinaceae, and Pucciniastraceae. Within the rust fungi, this type of aecia represents a unique character, and its exclusive occurrence on conifers (Pinaceae) leads to special adaptations of the parasites to their host plants.

Peridermioid aecia often occur late in summer or in autumn. In *Milesina*, the aecia are found about two or three months after the spermatogonia on needles of the current season. In *Hyalopsora*, the spermatogonia occur on needles of the previous season and the aecia on needles of the second previous season.

Spores in peridermioid aecia represent a unique character, too. They are often characterised by a smooth or nearly smooth strip from the apex to the base on one side of the spore. SEM images show these regularly arranged strips as longitudinal overlying structures or as areas with distinctly finer warts. The former have been observed in the genera *Chrysomyxa*, *Cronartium* or *Pucciniastrum*, the latter in the genera *Milesina* and *Uredinopsis* (see Zwetko and Blanz 2018).

(6) Roestelioid aecia are usually cornute-shaped. At first, their peridia are cylindrical and closed at the apex. At maturity, they generally tend to rip longitudinally. The time of maturity is uncommon. In spring (May or June) large, reddish spots with spermatogonia occur on the upper side of the leaves. These leaf spots increase and swell till the end of summer (August or September); then aecia are produced on the lower side of the leaf spots. The aeciospores exhibit an uncommon character, as well. Their walls are usually pigmented, with distinct scattered germ pores. The ultrastructure of the aeciospore surface has been analysed in detail by Lee and Kakishima (1999). The roestelioid aecium is characteristic of the genus *Gymnosporangium* and its anamorph *Roestelia*. It is produced on Rosaceae ('Maloideae').

According to their position in the life cycle, the following types of aecia are distinguished:

I: Aecia of endo-forms produce aeciospores which serve as probasidia and germinate with basidia at maturity.

Ia: Primary aecia are produced in association with spermatogonia.

Ib: Secondary aecia are repeating aecia, not in association with spermatogonia. Mostly, these kinds of aecia are produced by autoecious rusts, but in the genera *Chrysomyxa* and *Coleosporium* they replace the uredinia on the alternate host. Because of host alternation, most authors (even Gäumann 1959) defined these secondary aecia as uredinia, although their spores are formed in chains. According to their morphology, the secondary aecia of *Chrysomyxa* are peridermioid and those of *Coleosporium* caeomoid.

II: Uredinium (uredosorus, 'uredium')

In the evolution of rust fungi, the morphology of uredinia is less variable than that of aecia and telia, and the genus name '*Uredo*' has been used for the uredinial state of all rust fungi by many authors for a long time. Usually, this sorus is produced by a dikaryotic but sometimes also by a monokaryotic mycelium (primary uredinia). It bears urediniospores, which are one-celled and borne singly on pedicels; generally their walls are echinulate. The hilum, a scar on the spore at the point of attachment to the pedicel, is usually easily visible and distinguishes urediniospores from aeciospores. Uredinia occur on leaves, stems, fruits or fronds where the fungus often causes small yellow spots. Savile (1968) showed that Arthur's term 'uredium' is incorrect.

According to their gross morphology, the following main types of uredinia are distinguished:

(1) Uredinioid uredinia are usually subepidermal in origin, and erumpent, releasing a more or less pulverulent spore mass. This type of uredinia occurs in several groups of rust fungi, which are not closely related. Therefore, the following subdivision is somewhat tentative and perhaps of limited suitability:

- Uredinoid uredinia of the genus *Melampsora* are characterised by spores with unpigmented walls, bright orange-reddish contents and intermixed, persistent paraphyses also with unpigmented walls. Germ pores are difficult to observe. The peridium is soon evanescent, and the paraphyses are uniformly distributed throughout the sori.
- Uredinioid uredinia of the *Puccinia-Uromyces* complex bear spores with mostly pigmented walls, but the degree of pigmentation varies widely. In *Puccinia coronata*, for instance, the walls are nearly hyaline. Usually, the germ pores are visible in LM. The majority of *Puccinia* and *Uromyces* species lack paraphyses; in Europe only some graminicolous species like *P. arrhenatheri*, *P. brachypodii*, *P. deschampsiae* and *P. poae-nemoralis* possess persistent paraphyses. The paraphyses of *P. coronata* and *P. striiformis* collapse readily and are easily overlooked.
- Uredinioid uredinia of the *Sonchus* rust *Puccinia pseudosphaeria* (syn. *Peristemma p.*, *Miyagia p.*). In analogy to the terms applied for aecia, this type of uredinia could be named 'peristemmoid' uredinia.
- Uredinioid uredinia of the Rosaceae rust genus *Phragmidium* are usually surrounded by paraphyses, but a peridium is lacking. Cummins and Hiratsuka (2003) called such uredinia the '*Uredostilbe*-type'.

(2) Milesioid uredinia possess a delicate peridium, which is hemispherical or flat and opens by a regular or irregular pore, with or without distinct ostiolar cells. We have chosen this term in analogy to the terminology of aecia; Cummins and Hiratsuka (2003) called it '*Milesia*-type'. The pedicels of the urediniospores are often short and inconspicuous. Milesioid uredinia are typical of various genera of the Melampsorineae (except *Melampsora*, see above), e.g., *Thekopsora*, *Milesina*, *Melampsoridium* and *Pucciniastrum*.

According to their position in the life cycle, the following types of uredinia are distinguished:

IIa: Primary uredinia are produced in association with spermatogonia and replace the aecia.
IIb: Secondary uredinia are produced subsequently and independent from spermatogonia.

According to its position in the life cycle and and its different morphology, the following third type of uredinia is distinguished:

II*: Amphisporic sori (amphisori, amphioid uredinia) bear amphispores. The fern rust genera *Uredinopsis* and *Hyalopsora* and some *Puccinia* species on *Carex* have urediniospores of two kinds: thin-walled spores immediately germinating for propagation in summer, and so-called amphispores, urediniospores of the second kind, which have thicker walls and probably undergo a resting condition before germination. They are produced later for persistence. Spores intermediate between urediniospores and amphispores occur in some sori of, e.g., *Hyalopsora aspidiotus*. Amphispores differ from normal urediniospores also by their wall ornamentation.

III: Telium (teleutosorus)

Usually, this sorus is produced by a dikaryotic, but sometimes also by a monokaryotic mycelium (microcyclic rusts with spermatogonia). It bears teliospores. In temperate, alpine and arctic climates teliospores are mostly resting spores, which are capable of germination only after a period of winter dormancy. But in some genera (e.g., *Kuehneola*, *Leucotelium*, *Cronartium*, *Melampsorella*) and some species (e.g., *Phragmidium duchesneae*, *Puccinia arenariae*, *P. chrysosplenii*, *P. malvacearum*) germination occurs without dormancy. *Puccinia salviae* and some *Puccinia* species on the genus *Veronica* s.l. (like *P. albulensis*, *P. paederotae*, *P. veronicae-longifoliae*, and *P. veronicarum*) produce both kinds of teliospores, resting and non-resting spores. Such non-resting teliospores are also named ‘leptospores’ (but this term is often restricted to ‘lepto-forms’ – see below).

In most genera of rust fungi teliospores are arranged in sori, but in the genera *Uredinopsis*, *Milesina* and *Hyalopsora*, we find single, variably shaped spores or spore balls scattered in the mesophyll tissue or spores – uni- or multicellular by vertical septa – formed within the epidermis cells, but no well-organised sori. In *Melampsoridium* and *Melampsora*, the spores are grouped into a tight palisade or crust below the epidermis or the cuticula. The telium of the genus *Cronartium* consists of an erumpent long column of strongly adherent spores. “Increased exposure of the teliospores has evidently proved advantageous whenever it has occurred, for there is a steady trend in this direction, ... in several distinct evolutionary lines” (Savile 1955a: 87). All these genera have non-pedicellate teliospores. “Perhaps the greatest single advance in teliospore evolution was the initiation of spore pedicels. ... The pedicel may have developed in some lineages by specialisation of a cell of the mycelium on which the spore was borne. I suspect, however, that it generally developed ... by a transfer of the mechanism used in the uredinium: a meristematic basal cell cuts off a series of spore mother-cells, each of which divides into spore and pedicel” (Savile 1976: 158).

In the phylogeny of rust fungi, the morphology of aecio- and urediniospores remains rather constant, but the teliospores vary greatly in morphology. Therefore, the two anamorph states are easily distinguishable by morphological characters. Holm (1987: 434) agreed to the definition of teliospores by Hiratsuka (1973b): “The only workable definition of a teliospore is that it will form basidia upon germination”.

According to their position in the life cycle, the following types of telia are distinguished:

IIIa: Primary telia are often produced in association with aecia or primary uredinia, respectively.
IIIb: Secondary telia are not associated with aecia or primary uredinia.
III*: Basidiosori are interpreted in two different ways. Either as telia consisting of teliospores forming an ‘internal basidium’ at maturity (recognisable by insertion of three septa), or simply as sori consisting of basidia. We prefer the second interpretation. The most common examples are found in the genus *Coleosporium*, where the basidiosori appear as small, often red, wax-like crusts; except for their apex, the basidia of *Coleosporium* are thin-walled (Fig. 13, p. 194).

IV: Basidium (metabasidium)

Basidia and basidiospores are hardly ever described in detail, presumably rather uniform and of little diagnostic value. The basidium is normally a four-celled, transversely three-septate, straight or curved (meta-)basidium. Each cell develops a sterigma with a thin tip where the basidiospore is formed and finally released as a ballistospore with the help of Buller’s drop (e.g., Webster and Weber 2007), but there may be more exceptions than hitherto observed. Germination of basidia in basidiosori (see above) is somewhat divergent; in *Coleosporium*, each of the four cells of a basidium produces a long sterigma-like tube which breaks through the surface and forms a ballistospore at the tip.

Overview of life cycles

Based on the reduction of spore states, five main types of life cycles have been distinguished by European authors:

0, I, II, III, IV **Eu-form**
- Auteu-form, not host alternating

- Hetereu-form, host alternating; Jørstad (1964a) distinguished
  - obligate host alternating forms
  - facultative host alternating forms

0, I, III, IV **Opsis-form** (reduction of uredinia)
- Autopsis-form, not host alternating
- Heteropsis-form, host alternating

0, II, III, IV **Brachy-form** (reduction of aecia)

II, III, [IV?] **Hemi-form** (whole monokaryotic stage absent); this form is considered to be a hetereu-form originally, but alternation no longer takes place. Some rusts are known as hetereu-form, but in some areas alternation does not occur, and the telial stage is often suppressed. For other rusts considered as hemi-forms host alternation is not known at all.

(0), III, IV **Micro-form** (reduction of aecia and uredinia; forms with spermatogonia are rare)
- Typical micro-form with resting teliospores
- Lepto-form, with non-resting teliospores (leptospores; spore walls usually thinner and brighter than in resting teliospores)

Sometimes a sixth main type has been defined:

0, I, IV **Endo-form**; its aeciospores produce basidia and basidiospores upon germination.

Several variations and modifications of these main types exist in nature. Separate names for such variations are not helpful and would rather cause unnecessary complications. We have already used the Roman numerals like formulas (see above). With these symbols we can describe the life cycle of each rust species in detail, for instance:

(0, I), II, II*, III, IV	cycle of *Uredinopsis struthiopteridis*
0, I, [II], III, IV	cycle of *Puccinia firma*
I, II, III, IV	cycle of *Puccinia karelica*
I, [II], III, IV	cycle of *Puccinia rupestris*
0, I, II, IV	cycle of *Ochropsora anemones*
0, Ia, Ib, III, IV	cycle of *Chrysomyxa rhododendri*
0, Ia, Ib, IV	cycle of *Coleosporium tussilaginis*
(0?), Ia, IIIa, Ib, IIIb, IV	cycle of *Puccinia senecionis*
0, IIa, IIIa, IIb, IIIb, IV	cycle of *Puccinia punctiformis*
Ia, IIIa, [Ib], IIIb, IV	cycle of *Trachyspora alchemillae*
[Ia], IIIa, IV	cycle of *Trachyspora alchemillae* in N Europe and at higher altitudes
0, IIa, IIb, IIIb, IV	cycle of *Triphragmium ulmariae*
0, IIa, IIIa, IV	cycle of *Triphragmium ulmariae* at higher altitudes

In our descriptions of rust taxa, the Roman numerals and the names of the host plants are listed together. This arrangement shows at once whether a life cycle is obligatorily heteroecious (e.g., *Puccinia firma*), facultatively heteroecious (e.g., *Uredinopsis struthiopteridis*), or autoecious (e.g., *Puccinia senecionis*, *P. punctiformis*):

Puccinia firma
0, I on: *Bellidiastrum michelii*
[II], III, IV on: *Carex firma*

Uredinopsis struthiopteridis
(0, I on: *Abies alba*, *A. balsamea*)
II, II*, III, IV on: *Matteuccia struthiopteris*

Puccinia senecionis
(0?), Ia, IIIa, Ib, IIIb, IV on: *Senecio nemorensis* agg.

Puccinia punctiformis
0, IIa, IIIa, IIb, IIIb, IV on: *Cirsium arvense*

Nomenclature of rust fungi

In rust fungi, host alternation and the various types of sori and spores within one and the same life cycle were discovered quite soon, for instance, the identity of *Puccinia graminis* and *Aecidium berberidis* proven by De Bary (1865). This pleomorphism has a severe impact on rust fungi nomenclature, especially on the use of generic names.

Priority of names is regulated by Article 59 of the 'International Code of Nomenclature for Algae, Fungi, and Plants' (ICN), formerly the 'International Code of Botanical Nomenclature' (ICBN).

Before the implementation of the 'Melbourne Code' (ICN 2012), dual nomenclature for pleomorphic fungi was common practice, and the name of the telial stage (= teleomorph, sexual morph) had priority. For anamorphic (asexual) taxa with unknown life cycle, the anamorph names (e.g., in the form genera *Aecidium*, *Caeoma*, *Roestelia*, *Peridermium*, *Uredo*) remained in use, but they had to be replaced by the name of the telial stage after clarification of the complete life cycle or after determining the genetic relationship based on DNA studies, whereby the anamorphic names became synonyms.

At the International Botanical Congress in Melbourne in 2011, the 'one fungus = one name' principle was adopted thereby discontinuing the dual nomenclature for pleomorphic fungi. Consequently, since the Melbourne Code (ICN 2012) priority has to be given to the oldest validly described name, regardless of whether anamorphic or teleomorphic. At the same time the possibility to conserve names in common use was created. For this purpose, a proposal has to be published in the journal Taxon and accepted of the nomenclature committee at the next IBC, as is ongoing, e.g., for *Puccinia psidii*, to conserve this name against the competing anamorph names *Caeoma eugeniarum* and *Uredo neurophila* (Braun and Bensch 2022). Unless the worst cases can be alleviated

by such a conservation of some generic names, this rule will have devastating consequences on the nomenclature of rust fungi. For instance, *Aecidium* Pers. (1801: 204) would have priority over *Puccinia* Pers. (1801: 225). The number of new combinations from *Puccinia* to *Aecidium* would be breathtaking. According to Cummins and Hiratsuka (2003), *Puccinia* is the largest genus of rust fungi with 3000–4000 species, but these authors recognise very broadly defined species. The number of species considerably increases when applying a narrower species concept.

However, due to ongoing progress in taxonomic research, we will be facing quite a number of new combinations in the future, especially in the *Puccinia-Uromyces* complex. *Uromyces* is distinguished from *Puccinia* by its unicellular teliospores; in all other respects the two genera are similar. The number of cells in the teliospores in *Puccinia* is, however, not constant. Mesospores (one-celled teliospores) occur in several *Puccinia* species. In contrast, two-celled teliospores only rarely occur in *Uromyces* species. Arthur and others have suggested that the two genera should be combined. Using molecular genetic data, Van der Merwe et al. (2008) and Maier et al. (2007) have shown that the genera *Puccinia*, *Uromyces*, *Endophyllum*, *Cumminsiella* and *Miyagia* (= *Peristemma*) represent a highly supported monophyletic group of genera. On the other hand, the genera *Puccinia* and *Uromyces* emerged as polyphyletic and the degree of polyphyly was surprisingly high. From these analyses, it is clear that the number of cells in the teliospores does not have phylogenetic significance. Nevertheless, more species have to be included in molecular genetic studies before genera within the *Puccinia-Uromyces* group can be circumscribed satisfactorily. Therefore, *Puccinia* and *Uromyces* will most probably be treated in this rust flora (part 2, unpublished) sensu Cummins and Hiratsuka (2003).

On species level, nomenclatural problems in rust fungi do not really differ from those in other groups of organisms. Due to the highly divergent species concepts of different authors, however, it is often essential to cite a reference work or to give at least a rudimentary hint (e.g., 'sensu Gäumann 1959' or 'sensu lato') when using certain names. Probably the former nomenclatural priority of teleomorph names has somehow contributed to a broad, often uncritical circumscription of collective species in some groups (e.g., *Puccinia recondita* s. latiss. or *Melampsora populina* s. latiss.). Telia and teliospores of many rusts are rather poor in morphological characters and do not allow a satisfactory delimitation of species, e.g., in the fern rusts *Milesina* and *Uredinopsis*, or in many *Puccinia* species with sessile, smooth-walled teliospores. Consequently, also the characters of the other sori and spores in the life cycle were used for species delimitation. When also the host range is considered for the circumscription of species, this leads to a much narrower, 'biological' species concept, to infraspecific taxa (usually varieties), and finally to 'specialised forms' (formae speciales) with limited nomenclatural status. Under these circumstances, it is obvious that authors have to make clear whether they use a binomial for a morphologically delimited 'collective species' or for a narrowly defined 'biological species'.

The way of treating anamorphic form taxa of rust fungi is still unsatisfactory. Of course it is honourable and strictly in accordance with the ICN (2012, 2018) to get rid of (apparently unwelcome?) generic names like *Aecidium*, *Uredo* or *Caeoma* by pinning them down by 'types' and disposing of them in the synonymy of currently favoured generic names like *Puccinia* and *Uromyces*. At this point, however, it might be much more productive to dig up the types of anamorphic form species rather than those of form genera. Hundreds of names in *Aecidium*, *Uredo*, *Caeoma*, etc. are waiting for clarification; the generic name *Uredo* Pers. has even been used for describing and naming new form species in all groups of rust fungi for a long time, leaving us with a particular wealth of taxonomic challenges.

Arrangement of rust taxa, explanation of symbols and abbreviations, notes on the figures, and list of determination keys

Within their family all rust genera are listed alphabetically. Species are numbered within the genera and usually also arranged in alphabetical order, with few exceptions (e.g., the three major species complexes in *Melampsora*). Current names of rust taxa are given in ***bold italics***. Then all plant species occurring in Austria and previously recorded from Europe as hosts of rust fungi are listed under the respective rust taxa. The data are based on the literature. Poor knowledge on taxonomy, distribution, biogeography and ecology of rusts in natural habitats has been a limiting factor in accurately documenting European rusts (Helfer et al. 2011).

Many names of **rust taxa** had to be updated, following MycoBank (2024), Index Fungorum (2024), Thiel et al. (2023), and some recent taxonomic publications (e.g., Aime and McTaggart 2020). **Host plants** are named according to the checklist provided in the Austrian Red List of vascular plants by Schratt-Ehrendorfer et al. (2022).

As already mentioned above, the numerals **0, I, II, III, IV** are used as symbols for spermatogonia, aecia, uredinia, telia and basidia. Table 2 (p. 171) summarises the most important subtypes of the sori, their spores, and frequently encountered synonymous terms.

In the treatments of the rust species, **square brackets** indicate a tendency towards reduction or even total suppression of a spore stage. Spore stages not yet recorded from the area are given in **parentheses**, also host species so far unknown from the area. Information based on doubtful old literature or uncertain determinations is marked by '?'.

In the complementary **host-parasite index** for the present volume (Appendix 1, p. 330), all known host spe-

cies from the area are compiled alphabetically. Confirmed host-parasite combinations from Austria are given in ***bold italics***, those expected but not yet confirmed in *italics*. Uncertain affiliations or identifications are marked by '?', in line with the information given in the treatments of the rust species in the main chapter ('Rust taxa…').

Figures

Due to the changeful and peculiar history of the manuscript of this book, it would have been extremely tedious, in fact hardly possible to provide the illustrations with scale bars. For the structures figured in line drawings, LM and SEM micrographs, please refer to the measurements given in the descriptions of the species.

Unless stated otherwise, the habit photographs, close-ups and LM micrographs were made by Paul Blanz or Peter Zwetko. Photos by Julia Kruse are mostly published on the website '(Obligat) Phytoparasitische Kleinpilze' (Kruse 2024), The same applies for photos by Walter Obermayer which are partly published on the website 'Plants of Styria' (Obermayer 2024), but under the name of the host plant. For complete picture credits see Appendix 3 (p. 351).

Abbreviations

auct.	[sensu] auctorum [aliorum], in the sense of other authors (not according to the original description and/or the type material)
diam.	diameter
f.sp.	forma specialis, special form (an infraspecific category not covered by the ICN)
l.c.	loco citato, in the source cited immediately above
N.B.	nota bene (note well, note especially)
p.p.	pro parte, in part
s. …	sensu, in the sense of …
s.l.	sensu lato, in a broad sense
s. latiss.	sensu latissimo, in the widest sense
s.str.	sensu stricto, in a narrow sense
s. strictiss.	sensu strictissimo, in the narrowest sense
spp.	some or all species (of a genus)

A few acronyms of public herbaria from Index Herbariorum (Thiers 2024) are used.

List of determination keys

Key to the rusts on cone scales of *Picea* (p. 207)
Key to the *Melampsora* species on *Salix* (p. 214)
Key to rusts on *Euphorbia* (p. 228)
Key to the *Melampsora* species on *Salix caprea* when only uredinia are present (p. 233)
Key to the *Melampsora* species on *Populus* (p. 238)
Key to the *Melampsora* species on *Salix viminalis* (p. 243)
Key to the *Melampsora* species on *Salix retusa* (p. 245)
Key to the rusts on needles of *Abies* (p. 250)
Key to the *Melampsoridium* species in Europe (p. 263)
Key to the *Gymnosporangium* species on *Juniperus* in Central Europe (p. 273)
Key to *Gymnosporangium* species in the aecial stage (p. 274)
Key to the *Phragmidium* species on Rosa (p. 294)
Key to the rusts on *Rubus* in the aecial and uredinial stage (p. 305)
Key to the rusts on *Rubus* in the telial stage (p. 305)
Key to the *Trachyspora* species in Europe (p. 306)
Key to the rusts on *Prunus* in Europe (p. 312)
Key to the *Tranzschelia* species in Central Europe (p. 312)

Rust taxa: rust-host combinations, diagnoses, illustrations, remarks and keys

Several passages in the present book were still missing in the original manuscript of 2018 and have been supplemented by the second and third author (CS, IKG). Some of these are marked by insertions starting with the abbreviation **N.B.** ('nota bene') in bold, except for self-explanatory insertions of brief descriptions (of newly described or newly delimited families and genera) cited literally in quotation marks, mainly from Aime and McTaggart (2020). A few outdated passages in the original manuscript which had to be re-written (or re-arranged) are marked in the same way.

Melampsoraceae and related families (suborder Melampsorineae Aime)

In the present treatment, we adopt a narrower family concept supported by recent phylogenetic studies, mainly from Aime et al. (2018a) and Aime and McTaggart (2020).

The Pucciniales (formerly Uredinales) have been divided into only two families by Dietel (1928), Melampsoraceae and Pucciniaceae, a concept which was accepted by other authors for a long time. The Pucciniaceae usually have pedicellate teliospores, whilst the teliospores of Dietel's Melampsoraceae are non-pedicellate but otherwise rather variable including hardly detectable simple spores inside the mesophyll or inside the epidermis cells, as well as spores arranged in conspicuous flat crusts, chains or columns.

Based on aecia, uredinia, telia and host ranges, Dietel (1928) distinguished the five tribes Pucciniastreae, Cronartieae, Chrysomyxeae, Coleosporieae and Melampsoreae within the Melampsoraceae. Gäumann (1959) treated Dietel's five tribes as families. With the exception of the Pucciniastraceae, they were represented in Central Europe only by their type genera.

Hiratsuka and Cummins (1963) emphasised the importance of spermatogonia and recognised eleven morphological types. Based on these types, Cummins and Hiratsuka (1983, 2003) accepted 13 families worldwide, including Coleosporiaceae, Cronartiaceae, Melampsoraceae and Pucciniastraceae, but united Chrysomyxaceae with Coleosporiaceae. Aime (2006) expanded the Coleosporiaceae once more, incorporating also Cronartiaceae and Pucciniastraceae. Until now, neither the monophyly of the Pucciniastraceae nor of the Coleosporiaceae is well-supported by molecular data (Maier et al. 2003; Aime 2006; Aime and McTaggart 2020) and ultrastructure (Berndt 1993, 1996; Berndt and Oberwinkler 1995, 1997). Only the Melampsoraceae s.str. proved to be monophyletic and separate from the other families by a long genetic distance (Maier et al. 2003). Pei et al. (2005a, b) clearly demonstrated the close relation between the *Melampsora* species on the one hand and the comparatively loose connection with the other genera in this chapter, a finding confirmed by Aime (2006). In their study on *Chrysomyxa*, Feau et al. (2011) also showed that this genus is clearly distant from *Melampsora*.

Aecia are the most diverse sori of the Melampsorineae. Melampsoraceae s.str. are characterised by (often quite delicate) caeomoid aecia without a distinct peridium. In contrast, all other families (Coleosporiaceae, Milesinaceae, Pucciniastraceae) produce peridermioid aecia. Within the rust fungi, this type of aecia represents a unique character, and the fact that this type exclusively occurs on conifers gives evidence of the coevolution of host and parasite.

Peridermoid aecia are cylindrical, tongue- or blister-shaped, and the blister is often flattened in one plane. The peridium consists of relatively long and narrow, thick-walled cells arranged in one or several layers. It irregularly ruptures at maturity. In peridermioid aecia, the peridium forms by the differentiation of the distal-most cells of the aeciospore chain into the thick-walled peridial cells (Colley 1918; Littlefield and Heath 1979). This contrasts clearly with the mode of peridium morphogenesis in aecidioid aecia (*Puccinia-Uromyces* complex) where peripheral chains of aeciospores and intercalary cells differentiate to form the tubular peridium around the elongated aecia (Fromme 1914; Littlefield and Heath 1979). The lateral wall of the aecial peridium in *Puccinia* and *Uromyces* originates from aeciospore mother cells. But at least in some Melampsorineae its cells are the equivalents of aeciospores, and small residual intercalary cells may be encountered. This lateral wall is a structure that arose 'de novo' in the aecium under the necessity for a powerful thrust being exerted upon the epidermis (Savile 1955a). This author presented an interpretation for the different mode of peridium morphogenesis in peridermioid and aecidioid aecia: It is not certain that the original gymnospermous hosts had as tough an epidermis or cuticle as *Abies*, on which the contemporary fern rusts produce their aecia; but the very robust peridia of peridermioid aecia of most genera of the Melampsorineae show us the morphological adaption that was necessary. In the majority of angiospermous hosts rupture of the epidermis presents no great problem. In the *Puccinia-Uromyces* complex the principal function of the peridium is to maintain the pressure needed for forcible discharge of the aeciospores.

Zwetko and Blanz (2018) showed that the mechanical problem of rupture of the epidermis on gymnospermous hosts characterises not only the morphology and morphogenesis of the aecial peridium but also the morphology of the aeciospores. Zwetko and Blanz (2018) compared spores in aecidioid aecia with spores in peridermioid aecia. In aeciospores of aecidioid aecia of the *Puccinia-Uromyces* complex, the aeciospore wall is distinctly trizonate in certain species, with a circular, almost smooth, only finely verrucose apical cap, a broad lateral belt with more or less coarse warts (sometimes with dehiscent pore plugs), and a finely verrucose basal hemisphere (Zwetko and Blanz 2012). In contrast, aeciospores from peridermioid aecia show a peculiar longitudinal structure, i.e., a broad smooth strip from the apex to the

base of the spore. Klebahn's (1914) excellent drawings already show such a smooth strip on aeciospores in the genera *Cronartium*, *Melampsoridium* and *Pucciniastrum* s.l., and his observations were confirmed by several other authors who studied one or more genera (e.g., Peterson 1967; Hiratsuka 1971; Kaneko 1981; Hiratsuka and Sato 1982; Sato and Sato 1982; Crane 2001). In a study on *Chrysomyxa*, Crane (2001) was apparently the first who described the longitudinal structure as an occasionally groove-like overlay on one side of the aeciospore connecting two narrow, irregular caps. Zwetko and Blanz (2018) confirmed this finding in their SEM studies of aeciospores of *Thekopsora areolata*, *Chrysomyxa rhododendri* and *Cronartium flaccidum*. Moreover, they stated that the broad longitudinal strip with distinctly finer warts on the aeciospores of *Milesina* and *Uredinopsis* can be interpreted as a homologous structure.

Such smooth longitudinal structures are absent on the aeciospore walls of other rust genera. For instance, Littlefield and Heath (1979) described and illustrated the ultrastructure of the aeciospore wall and its development in *Melampsora lini* and *Puccinia recondita*. In immature aeciospores of *Melampsora lini* (s.l.) a mucilage-like interstitial matrix between warts appears to condense or to break down, exposing evenly spaced ornaments (warts) over the whole surface of the spore. A similar process occurs in *Puccinia recondita*, although the interstitial matrix lacks the mucilage-like appearance of that in *M. lini*. SEM photos of young aeciospores of *P. recondita* in Littlefield and Heath (1979) show an irregular and variable interstitial matrix (primary spore wall) covering the wall ornaments. The interstitial matrix disappears at an early stage, and the ornaments of mature *P. recondita* aeciospores are fully exposed. The smooth, more or less circular apical cap of the aeciospore wall (which is typical of many taxa in the *Puccinia-Uromyces* complex) does not disappear at maturity (Zwetko and Blanz 2012).

Another distinct feature of the aeciospore wall of Coleosporiaceae, Milesinaceae and Pucciniastraceae is the 'annulate' structure of the wall ornaments (warts) proper which are built of two to several stacked discs, sometimes tapering towards the top; moreover, these stacks are longitudinally furrowed in some taxa. Zwetko and Blanz (2018) figured a remarkable 'gradation' among the wall ornaments of Melampsorineae on conifers: In *Chrysomyxa rhododendri* (and many others) the ornaments of the (primary) aeciospores consist of several stacked disks, in *Rossmanomyces pyrolae* they are built of two cushion-like discs on a stout base, and in *Melampsora laricis-epitea* they consist of only two elements, a stout base and one globose structure on top (Figs 8d, 19b, 23 on pages 186, 204, 208).

In the evolution of rust fungi, the morphology of **uredinia** is less variable than that of aecia and telia. Urediniospores are borne singly on pedicels and mostly echinulate. The uredinia of several genera within the Melampsorineae are covered by a hemispherical or flat peridium, opening by a regular or irregular pore with or without clearly differentiated ostiolar cells. In *Melampsora*, the peridium is soon evanescent, and the sori possess abundant, persistent paraphyses, which are uniformly distributed throughout the sori. The spore walls in *Melampsora* are hyaline, and the germ pores are usually invisible. Special methods of preparation are needed to study the pores (see Kaneko and Hiratsuka 1982).

For the morphological characters of **telia**, see the various families and genera of the Melampsorineae.

Coleosporiaceae Dietel emend. Aime & McTaggart (incl. Chrysomyxaceae Gäum. ex Leppik, Cronartiaceae Dietel)

Recent circumscriptions of the Coleosporiaceae are provided by Hardtke et al. (2021) and Aime and McTaggart (2020). Currently the family comprises some genera of conifer rusts previously separated in different families by morphological characters and host range, especially Chrysomyxaceae and Cronartiaceae (e.g., Gäumann 1959). Inclusion of Cronartiaceae was suggested by Aime (2006), transfer of *Thekopsora* from Pucciniastraceae by Aime et al. (2018a). Consequently, this family is very diverse from the morphological point of view but also in the host ranges of the genera. The 'uredinia' of *Chrysomyxa*, *Rossmanomyces* and *Coleosporium* formed on the telial hosts after alternation are actually secondary aecia, recognizable by secondary aeciospores which are produced in chains. Telia are rather diverse, teliospores mostly not dormant. The 'telia' of *Coleosporium*, however, are basidiosori, and their 'teliospores' are regarded as basidia here. Most species are heteroecious and macrocyclic, with some derived microcyclic or probably endocyclic species. Uredinia/secondary aecia and telia/basidiosori of Coleosporiaceae are found on plants of various families of dicotyledons.

Chrysomyxa Unger

The small genus occurs in the N temperate region (Europe, Asia and N America). It is usually host alternating (except for derived species like the micro-form *Ch. abietis*) and produces spermatogonia and primary aecia on *Picea*, and secondary aecia and telia on Ericaceae s.l. (incl. Empetraceae). Because of host alternation, most authors (e.g., Gäumann 1959; Klenke and Scholler 2015) defined the secondary aecia as uredinia, and we add this alternative interpretation in parentheses. Radial sections through the lateral part of secondary aecia of *Chrysomyxa empetri* and *Ch. rhododendri* show that the development of spores and peridium starts from short chains of cells of which the apical cells transform into peridial cells (Berndt 1999b). This type of spore and peridium formation characterises peridermioid aecia. – **Spermatogonia** amphigenous on needles, subepidermal (Group I, type 2, according to Cummins and Hiratsuka 2003). – **Primary aecia** peridermioid, subepidermal in origin, erumpent; peridium well-developed, membranous, consisting of a single layer of cells and dehiscing irregularly at the apex. – **Primary aeciospores** catenulate with intercalary cells;

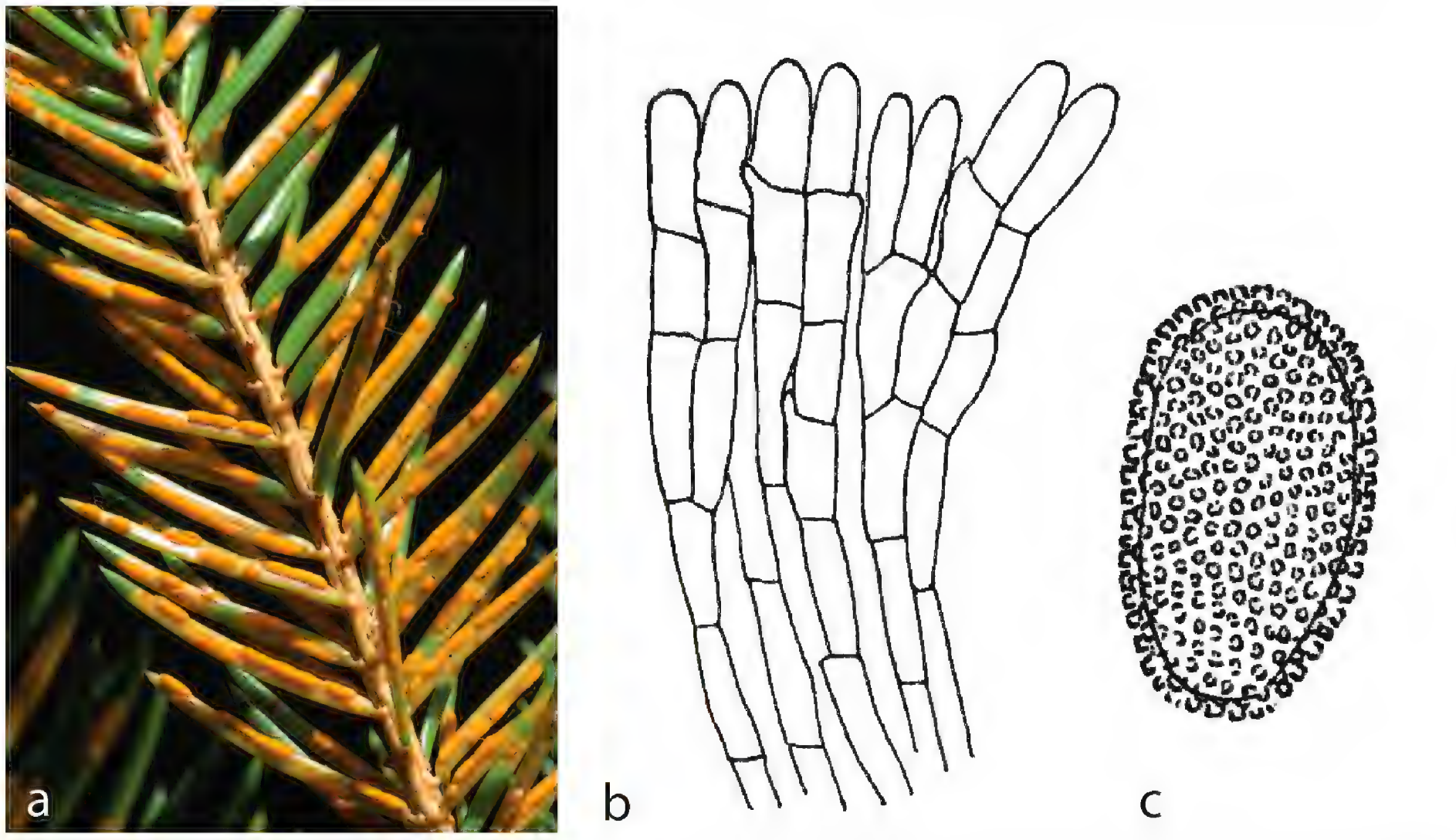


Figure 6. *Chrysomyxa*. **a, b.** *Ch. abietis* on *Picea abies*: **a.** Twig with infected needles bearing cushion-like telia; **b.** Teliospore chains; **c.** *Ch. empetri* on *Empetrum nigrum*: secondary aeciospore; (**a** by Dan Aamlid, with permission; **b, c** from Klebahn 1914: 722).

wall hyaline, coarsely warted, often with a longitudinal, smooth strip; warts (ornaments) annulate. – **Secondary aecia (uredinia)** peridermioid, subepidermal, erumpent, pulverulent, with or without a very delicate peridium. – **Secondary aeciospores (urediniospores)** catenulate, formed in basipetal succession together with intercalary cells, resembling primary aeciospores. – **Telia** subepidermal in origin, erumpent, pulvinate, waxy. – **Teliospores** in simple or branching chains, 1-celled, with thin, hyaline walls, not separated by intercalary cells, germinating without dormancy. – **Basidia** are formed by elongation of the apex of uppermost teliospores or between the loose and mostly collapsed outermost spores.

Dietel (1928) suggested that *Chrysomyxa* is related to *Thekopsora* because both genera occur on Ericaceae. Gäumann (1959) defined two 'form groups' (Formenkreise) within the genus, based on host range and infestation behaviour. The first group (*Ch. rhododendri* group) includes species with (±) localised haplophase mycelium on spruce needles and dikaryotic phase on Ericaceae: *Ch. empetri*, *Ch. ledi*, *Ch. rhododendri*, and the micro-form *Ch. abietis*. The second (*Ch. pirolatum* group), has recently been separated as the genus ***Rossmanomyces*** and includes species with (±) systemic haplophase mycelium on the cone scales of spruce and dikaryophase on Ericaceae subfam. Pyroloideae (syn. Pyrolaceae): *R. monesis*, *R. pyrolae* (syn. *Chrysomyxa pirolatum*), and *R. ramischiae*. Savile (1950) emphasised the importance of the size and spacing of the warts on the surface of aeciospores in distinguishing the species.

In Central Europe, *Chrysomyxa* species are mainly distributed in the montane forests of the Alps and the low mountain ranges. The wax-like crust-forming telia develop on overwintering leaves.

1 *Chrysomyxa abietis* (Wallr.) Unger

Fig. 6a, b

Syn. *Blennoria abietis* Wallr.

Micro-form:

III on: *Picea abies*, (*P. engelmannii*, *P. pungens*, *P. sitchensis*)

Spermatogonia absent. – **Telia** on transverse orange or yellow bands on the needles, hypophyllous, elongate, 0.5–10 mm long, 0.3–0.5 mm broad, 0.5 mm high, orange to reddish-brown. – **Teliospores** in chains 70–120 µm long, single spores 20–30 × 10–14 µm, oblong; wall hyaline, smooth, 1 µm thick; contents orange; basidium 4-celled. – References: Gäumann (1959: 101), Wilson and Henderson (1966: 59).

Remarks. The hyphae of *Chrysomyxa abietis*, growing first in the intercellular space of the mesophyll, invade also the mesophyll cells in autumn, and start producing teliospores (Grill et al. 1984). The spores mature in spring and germinate without any period of rest. This rust may cause considerable defoliation of spruce. The infection is heaviest in dense stands of young trees.

This rust is also recorded on *Picea engelmannii*, *P. pungens* and *P. sitchensis* from Norway, Scotland and Ireland (Wilson and Henderson 1966; Gjærum 1974). According to Gäumann (1959), these records need revision. In N America *P. engelmannii* and *P. pungens* serve as hosts of the similar *Ceropsora weirii* (H.S. Jacks.) Aime & McTaggart (syn. *Chrysomyxa w.*). Its life cycle resembles that of *Ch. abietis*. – For the distribution of *Ch. abietis* in Austria see Poelt and Zwetko (1997: 48).

2 *Chrysomyxa empetri* (Pers.) J. Schröt.
Fig. 6c

Heteropsis-form with secondary aecia:
(0,Ia on: *Picea abies*?, *P. glauca*)
Ib,III on: *Empetrum hermaphroditum*, (*E. nigrum*)

Spermatogonia on needles of current season, amphigenous, in one row, conspicuous, yellowish then reddish-brown, subepidermal, 140–160 µm broad, 100–135 µm deep. – **Primary aecia** on needles of current season, amphigenous, in one row, on pale-yellowish portions, elliptical to subcircular in transverse section, 0.5–1.5 mm wide, 0.5–2 mm high; peridium hyaline, rupturing at apex; peridial cells 19–54 × 32–76 µm, polygonal, elongate vertically; outer walls smooth, about 1 µm thick, inner walls coarsely verrucose, 4–5 µm thick. – **Primary aeciospores** 21–34 × 30–47(–55) µm, ellipsoid or ovoid, yellow; wall closely and coarsely verrucose, 0.3–1.5 µm thick excluding the warts. – **Secondary aecia** (uredinia) epiphyllous, one or few on a leaf, pustular, subepidermal, circular or elliptical to linear, 0.2–2 mm long; peridium distinct, adhering to the epidermis which ruptures at maturity; peridial cells in a single layer, angular, 10–20 µm in diam.; wall 3–4 µm thick. – **Secondary aeciospores** (urediniospores) catenulate, 25–49 × 20–31 µm, pulverulent, ellipsoid, ovoid or subgloboid, orange; wall hyaline, closely and coarsely verrucose, 0.2–1 µm thick, excluding the warts; warts cylindrical to slightly stellate or irregular, 0.7–2.2 µm high, 0.3–1.0 µm wide, 0.7–2.5(–3) µm spacing. – **Telia** epiphyllous on overwintered leaves, one or few on a leaf, yellow, cushion-shaped, wax-like, subepidermal, subcircular to elongate, often nearly as long as the leaf. – **Teliospores** catenulate, 3–6 in a chain, 19–24 × 18–21 µm, thin-walled, smooth; contents yellow. – **Basidia** 4-celled, pale yellow, up to 65 µm long, 7–8 µm in diam. – **Basidiospores** 10–15 µm in diam., usually about 12 µm, subgloboid to ellipsoid, very thin-walled, with yellow contents. – References: Gäumann (1959: 99–101), Wilson and Henderson (1966: 60), Termorshuizen and Swertz (2011: 158).

Remarks. According to Gäumann (1959), *Chrysomyxa empetri* is widespread in Eurasia and N America, but telia are recorded rather infrequently; in some areas only secondary aecia are known. – For records of *Ch. empetri* in Austria see Poelt and Zwetko (1997: 48–49).

3 *Chrysomyxa ledi* (Alb. & Schwein.) de Bary
Fig. 7

Syn. *Chrysomyxa ledi* (Alb. & Schwein.) de Bary var. *ledi* s. Savile (1950, 1955b)

Heteropsis-form with secondary aecia:
(0,Ia on: *Picea abies*, *P. engelmannii*, *P. glauca*, *P. mariana*)
Ib,III on: *Rhododendron tomentosum*? [syn. *Ledum palustre*]

Spermatogonia on current-year needles, single or in small groups, amphigenous, subepidermal, 100–190 µm wide, 90–150 µm high, orange coloured, in median section concave to slightly flattened. – **Primary aecia** on current-year needles, amphigenous, in one or two longitudinal rows, on yellow spots, tubular, 0.3–1.3 mm wide; peridium dehiscing at apex, later shredding, leaving a fringe around the sorus; outside of cells deeply concave, ± smooth; inside of cells shallowly concave, shallowly and densely warted, warts often arranged in undulating rows; lateral margins broad (3–6 µm or more) with coarse striations. – **Primary aeciospores** 20–38 × 15–28 µm (x = 28.0±4.1 × 21.6±2.4 µm), ovoid, ellipsoidal, globose, or subglobose, with a distinct narrow longitudinal groove; wall hyaline, 0.8 µm thick; wall plus warts 1.6–4.9 µm thick; warts crowded, annulate, tapering. – **Secondary aecia** (uredinia) hypophyllous on leaves of previous year, orange-red, later fading, occasionally caulicolous, circular, 0.2–0.3 mm wide, single or in groups; peridium of two or three layers of thin-walled pseudoparenchymatous cells that are much smaller than spores. – **Secondary aeciospores** (urediniospores) 18–30 × 16–26 µm (x = 24.2±1.7 × 20.7±1.3 µm), globose, subglobose or ovoid, occasionally ellipsoidal, sometimes notched or flattened at one end because of a narrow longitudinal groove with or without a well-defined edge; wall hyaline, 0.5–0.8 µm thick; wall plus warts 2.5–2.9 µm thick. – **Telia** hypophyllous on leaves of previous year, sparsely aggregated, flat, blood red to orange-red. – **Teliospores** catenulate, 5–7 in a 70–90 µm long chain, 13–30 × 10–20 µm, oblong to cuboid; contents orange. – **Basidiospores** 11 × 7 µm, ovoid; contents orange. – References: Gäumann (1959: 96–97), Crane (2001: 965–966).

Remarks. *Chrysomyxa ledi* occurs in Eurasia throughout the range of its broad-leaved hosts, independent of host alternation, in N Europe on *Rhododendron tomentosum* Harmaja (syn. *Ledum palustre*). The aecial stage is found on native and ornamental spruces, in Europe on *Picea abies*, *P. obovata*, *P. engelmannii*, *P. glauca*, *P. mariana*, and probably others (Crane 2001). *Chrysomyxa ledi*, the Eurasian hypophyllous rust on *Rhododendron tomentosum*, is distinct in morphology from the rusts occurring on *Rhododendron* subsect. *Ledum* in N America. SEM clearly demonstrates the morphological differences, especially of primary and secondary aeciospores, distinguishing *Ch. ledi* s.str. from the N American taxa, treated as separate species by Crane (2001). Five specimens from Japan (PUR) on several varieties of *Ledum palustre* (now all considered as *Rhododendron diversipilosum*) were examined by Hiratsuka et al. (1992); they also differ somewhat from the European specimens and were therefore not used to compile the species description. Their secondary aeciospores are smaller (14–25 × 11–21 µm, x = 19.4±2.7 × 14.9±2.2 µm) than those in European samples and their surface ornamentation is variable (l.c., figs 4B, 4D). Warts have broad irregular tops, and spores may have a flattened end where warts are confluent; however, there is seldom a well-defined groove. The coarser margins of

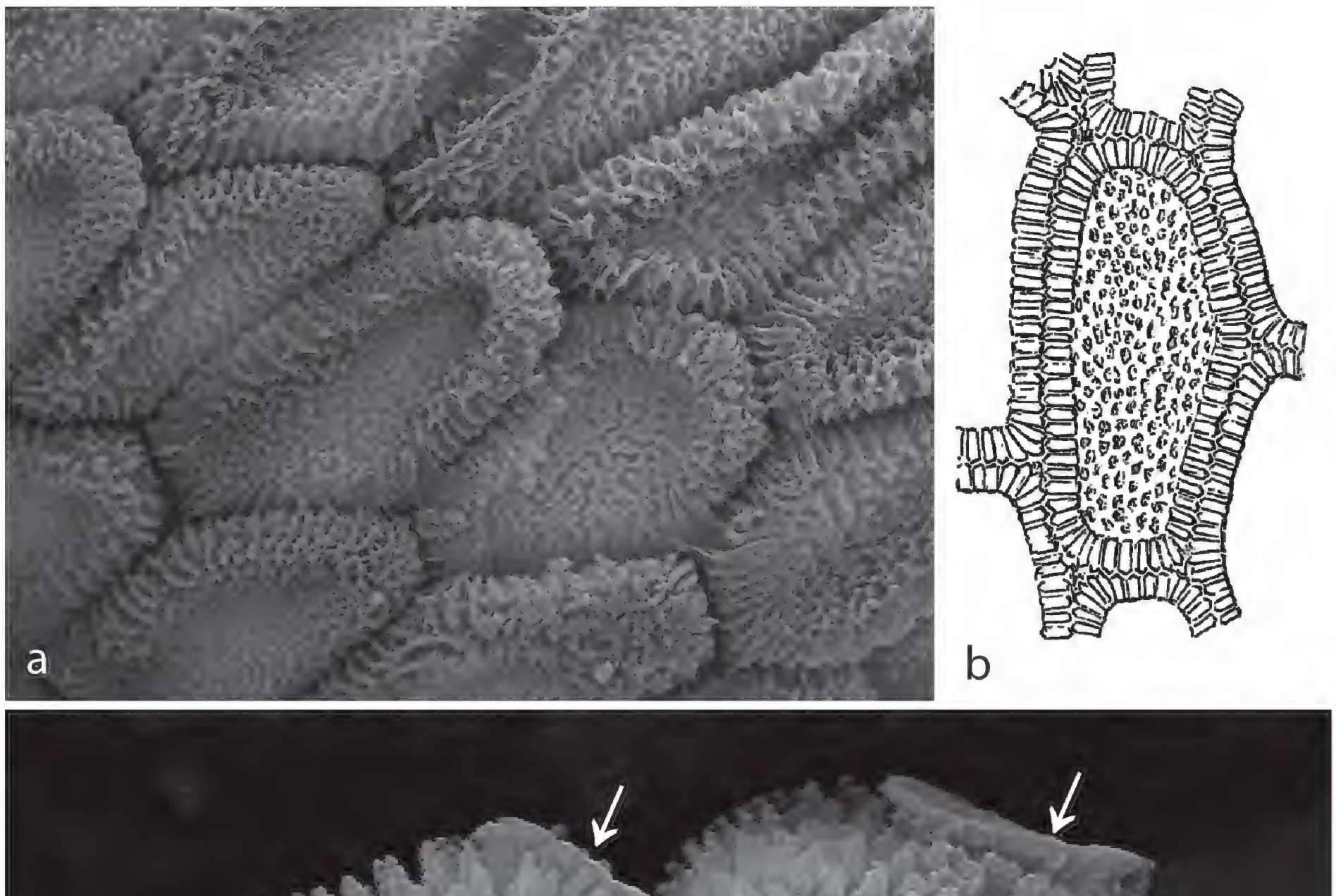
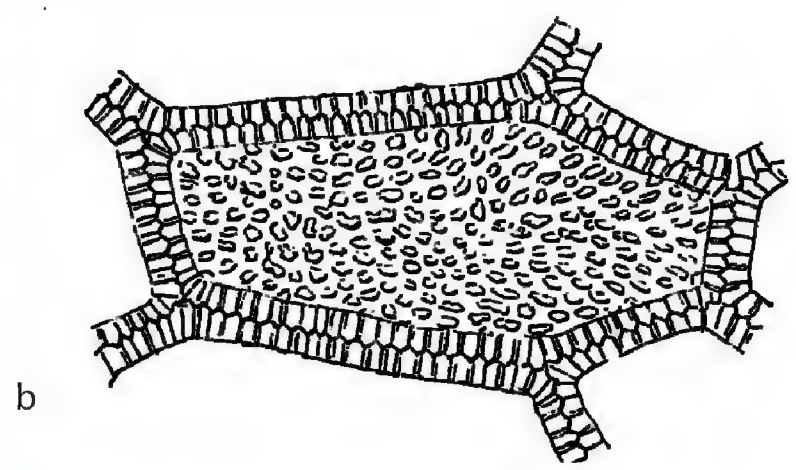
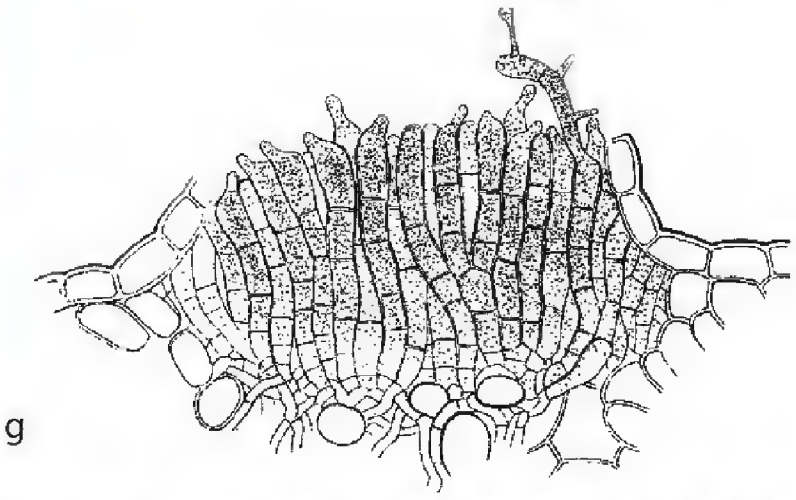


Figure 7. *Chrysomyxa ledi* on *Picea abies*: **a.** Inner surface of interlocking peridium cells of a primary aecium in SEM; **b.** Same view of a peridium cell in a line drawing; **c.** Two primary aeciospores in SEM, note the tapering annulate wall ornaments and the cap-like structures (arrows) formed by the ends of the smooth overlay of the spore wall, compare Fig. 8c; (**a, c** from Zwetko and Blanz 2018: 278, 276; **b** from Klebahn 1914: 692).

the peridial cells of *Ch. ledi* (l.c., fig. 4H) are an important distinguishing feature between the aecial stages of *Ch. ledi* and *Ch. rhododendri*. Although *Ch. ledi* is not known to occur in N America, certain morphological features of rusts on *Rhododendron* subsect. *Ledum* from both continents suggest a common ancestor. The peridial cells of *Ch. ledi* are remarkably similar to those of *Ch. ledicola* (Peck) Lagerh. in N America (Crane 2000), and the peridium of both species shreds in a similar manner during aeciospore release. *Chrysomyxa ledi* and *Ch. woroninii*





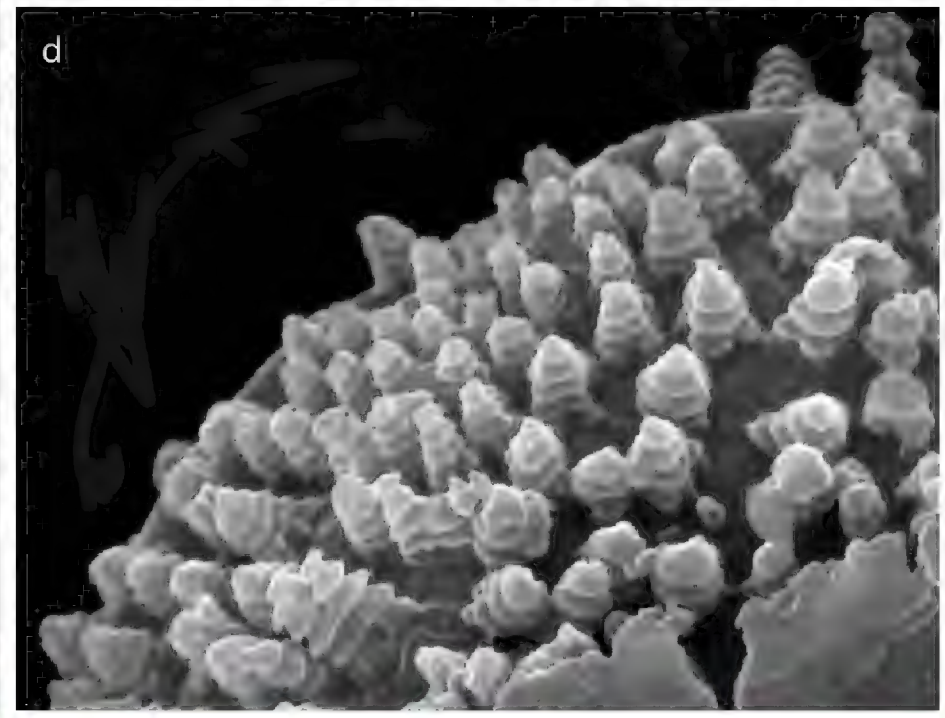


Figure 8. *Chrysomyxa rhododendri*. **a–d.** On *Picea abies*: **a.** Needles with primary aecia; **b.** Inside of peridial cell of primary aecium; **c.** Single primary aeciospore with a longitudinal groove-shaped overlay with warts (ornaments) underneath (arrow); **d.** Annulate ornaments at higher magnification; **e–g.** On *Rhododendron*: **e.** Groups of orange-yellow secondary aecia (uredinia) on *Rh. ferrugineum*; **f.** Telia on *Rh. hirsutum*; **g.** Median section through a telium with a few teliospores starting germination; (**a** by Walter Obermayer; **b** from Klebahn 1914: 692; **c, d** from Zwetko and Blanz 2018: 276, 280; **e, f** by Julia Kruse; **g** from Dietel 1928: 44, after De Bary, with permission from Duncker & Humblot GmbH).

occur on the same host plants, but they cause different signs and symptoms on both hosts, *Rhododendron* subsect. *Ledum* and *Picea* (Crane et al. 2000; Crane 2001). In N Europe, rainy summers favour heavy infection of spruce by *Ch. ledi* (Melekhov 1946), and trees over large areas may turn bright yellow. Premature shedding of needles probably affects incremental growth. – For a record of *Ch. ledi* in Austria see Poelt and Zwetko (1997: 49).

4 *Chrysomyxa rhododendri* (DC.) de Bary

Fig. 8

Syn. *Chrysomyxa ledi* s.l.; *Ch. ledi* (Alb. & Schwein.) de Bary var. *rhododendri* (de Bary) Savile

Heteropsis-form with secondary aecia:
0,Ia on: *Picea abies*, (*P. pungens*)
Ib,III on: *Rhododendron ferrugineum*, *R. hirsutum*, (*R.* ×*intermedium*, *Rhododendron* spp. cult.)

Spermatogonia on current-year needles, amphigenous, numerous, prominent, round or elongated, honey-coloured, then reddish-brown; hymenium broad and flat to shallowly concave in vertical section, 140–220 µm wide and 110–150 µm high. – **Primary aecia** on transverse, yellowed zones of current-year needles, causing premature defoliation, amphigenous, variable in size, 0.3–1.3 mm wide, up to 3 mm long, single or confluent; peridium delicate, irregularly torn at maturity but persistent, white; on outside, cells shallowly concave, smooth; on inside, cells convex with shallow warts, sometimes appearing labyrinthine; lateral margins narrow (about 2 µm), striate. – **Primary aeciospores** 18–30 × 16–22 µm (x = 23.6±2.7 × 18.6±1.5 µm), variable in shape from globoid to ellipsoid or ovoid, with one or both ends flat or with a small delicate cap, part of an indistinct longitudinal, smooth strip containing irregular shallow bumps (not always visible by light microscopy); wall hyaline, wall plus warts 2.0–3.3 µm thick; contents orange. – **Secondary aecia** (uredinia) hypophyllous on leaves of previous year, also on petioles, fruit pedicels and twigs, scattered, partially or completely covering underside of some leaves but absent from others, erumpent through epidermis, round, pulvinate, 0.2–0.7 mm wide, larger on twigs, flat-bottomed in vertical section; peridium inconspicuous, of collapsed, thin-walled cells. – **Secondary aeciospores** (urediniospores) 18–32(–36) × 14–22 µm (23.6±3.0 × 17.7±2.0 µm), mostly ellipsoid or ovoid, occasionally globoid, one or both ends slightly flattened or with a small cap which is part of a shallow longitudinal strip containing shallow, irregular bumps; contents apricot-coloured; wall hyaline, less than 1 µm thick; wall plus warts 1.2–2.9 µm thick. – **Telia** hypophyllous on leaves of previous year, in groups, confluent, erumpent through epidermis, larger and more irregular in shape than the secondary aecia, up to 1 mm long. – **Teliospores** catenulate (chains 4–6-celled in the middle of the sorus), cylindric-prismatic, 20–30 µm long, 10–14 µm wide. – References: Gäumann (1959: 94–95), Wilson and Henderson (1966: 62–63), Crane (2001: 974–975).

Remarks. Some authors synonymised *Chrysomyxa rhododendri* with *Ch. ledi* (e.g., Termorshuizen and Swertz 2011), and Savile (1950, 1955b) reduced *Ch. rhododendri* to a variety. On the other hand, Crane (2001) noted that the mean size of secondary aeciospores of *Ch. ledi* and *Ch. rhododendri* is very similar, but the primary aeciospores of *Ch. ledi* tend to be longer than those of *Ch. rhododendri*. Whereas *Ch. ledi* spores have a narrow groove and long tapered warts, those of *Ch. rhododendri* have an indistinct smooth or irregular longitudinal strip and only somewhat conical warts (Fig. 8c, d). The habitat differences also support the separation of these two taxa as distinct species: *Ch. rhododendri* occurs mainly in subalpine regions in Europe, *Ch. ledi* at lower elevations farther north. – For the distribution of *Ch. rhododendri* in Austria see Poelt and Zwetko (1997: 49–50).

(5) *Chrysomyxa woroninii* Tranzschel

Heteropsis-form (without secondary aecia):
(0,Ia on: *Picea abies*, *P. glauca*, *P. mariana*, *P. pungens*)
(III on: *Rhododendron tomentosum* [syn. *Ledum palustre*])

Spermatogonia not described. – **Primary aecia** on unfurling shoots resembling a cone or a stunted witches' broom, golden yellow, densely and evenly distributed over the whole surface of pale, fleshy, patent needles. – **Primary aeciospores** (27–)33–62(–66) × (16–)21–30(–45) µm. – **Telia** already appearing in spring on shoots resembling a small witches' broom, densely covering the young leaves of shooting buds. – **Teliospores** similar to those of *Ch. ledi*. – References: Crane et al. (2000: 584–586), Klenke and Scholler (2015: 689–690).

Remarks. Crane et al. (2000) clarified the life cycle of *Chrysomyxa woroninii* and found that it has no secondary aecia (uredinia). Infected spruce buds need almost one year before they show the typical symptoms. This rust is not listed by Poelt and Zwetko (1997) and has not been found in Central Europe so far; its distribution is circumpolar.

Coleosporium Lév.

N.B.: Descriptions of *Coleosporium* species (except for *C. tussilaginis* s.l.) were missing in the original manuscript and supplemented in line with the species concept favoured by Peter Zwetko, following Gäumann (1959).

Coleosporium species are predominantly heteroecious with spermatogonia and primary aecia on the needles of *Pinus*, and secondary aecia and basidiosori on various families of angiosperms, especially Asteraceae. Many authors (e.g., Gäumann 1959; Klenke and Scholler 2015) define the secondary aecia as uredinia, and the basidiosori as telia (see remarks). Therefore, we prefer to add these alternative interpretations in parentheses.

Central European taxa were often united in a single species complex usually named '*Coleosporium tussilaginis* s. latiss.' or '*C. tussilaginis* s.l.' (s. Hylander et al. 1953; Brandenburger 1985; Termorshuizen and Swertz 2011, and others). Also Helfer (2013), in his critical assessment of European taxa and their distribution, accepted only formae speciales within this taxon. Beenken et al. (2017) presented molecular phylogenetic evidence for at least three distinct species complexes (or three ± broadly defined species, respectively): *C. pulsatillae*, *C. inulae*, and *C. tussilaginis*. For the time being, we prefer to maintain the narrowly delimited species accepted by Gäumann (1959) which are chiefly defined by host specificity in the dikaryotic stage. *Coleosporium* records on pines can only be assigned to a particular species by inoculation experiments, by unambiguous field observations, or by molecular genetic evidence. – **Spermatogonia** subepidermal, with paraphyses and flexuous hyphae (Group I, type 2 according to Cummins and Hiratsuka 2003). – **Primary aecia** peridermioid, foliicolous, erumpent, with prominent, tongue-shaped peridia composed of a single layer of verrucose cells, dehiscing irregularly (Fig. 9a). – **Primary aeciospores** catenulate, ellipsoid or globoid, with hyaline, tessellate, superficially tuberculate wall (Figs 9b, 11). – **Secondary aecia (uredinia)** caeomoid, usually hypophyllous, subepidermal, erumpent, pulverulent, without peridia (Fig. 10). – **Secondary aeciospores (urediniospores)** catenulate, globoid or oblong, in wall structure resembling the primary aeciospores (Fig. 12). – **Basidiosori (telia)** usually hypophyllous, subepidermal, indehiscent except through weathering, flattened, at first forming wax-like crusts, becoming gelatinous on germination (Fig. 10). – **Basidia (teliospores)** sessile, in a single layer in lateral contact, cylindroid, clavoid or prismatic with smooth, hyaline walls, thin at the sides, strongly thickened and gelatinous above, at first unicellular, then becoming divided into four cells, each producing a long sterigma bearing a basidiospore (Figs 13, 14). Germination occurs without dormancy in summer and autumn. – **Basidiospores** ovoid or ellipsoid, rather large, thin-walled, reddish-orange.

Remarks. *Coleosporium* species do not have true teliospores but basidia produced in telium-like crusts (basidiosori) beneath the host epidermis (e.g., Berndt 1996). The basidium is also interpreted as a teliospore (probasidium) forming an intracellular metabasidium by 'internal germination' (e.g., Gäumann 1959; Klenke and Scholler 2015). Wall ornamentation of primary aeciospores is rather diverse in this genus (e.g., Hiratsuka and Kaneko 1975; Kaneko 1981), but not in the European species of the *C. tussilaginis* complex (see below).

Figure 9. *Coleosporium tussilaginis* s.l. **a1, a2.** Primary aecia on needles of *Pinus sylvestris*; **b.** Primary aeciospore in SEM showing the column-like, annulate wall ornaments. Scale bar: 2 µm (**a** by Walter Obermayer; **b** from Helfer 2013: 91, with permission from the author and Mycotaxon Ltd.).

Two remarkable neomycetes of this genus were recorded from Austria rather recently, ***Coleosporium montanum*** (Arthur & F. Kern) McTaggart & Aime on *Symphyotrichum novae-angliae* (Voglmayr et al. 2020), most probably also on *S. lanceolatum* (Scheuer 2015, 2018, as *C. asterum*), and ***C. solidaginis*** (Schwein.) Thüm. on *Solidago gigantea* (Voglmayr et al. 2022). For an assessment of European records of *C. solidaginis* see Beenken et al. (2017).

1 *Coleosporium tussilaginis* s.l. (s. Hylander et al. 1953 and others)

Fig. 9

Syn. *Peridermium oblongisporum* Fuckel s.l.

Heteropsis-forms with secondary aecia (or life cycle insufficiently known):

0,Ia on: *Pinus sylvestris*, *P. mugo*, *P. nigra* and other two-needle pines (also cultivated species)

Collections on the following hosts could not be assigned to any known *Coleosporium* species within this complex:

(Ib,III* on: *Clematis* sp. cult., *Erechtites hieraciifolius*, *Tropaeolum* sp. cult.)

Spermatogonia on needles, amphigenous, chiefly epiphyllous on pale or yellow spots, subepidermal or subcortical, scattered or in two longitudinal rows, yellowish, becoming brown, conoid, flattened, 0.5–1 mm long, 0.2–0.5 mm wide. – **Primary aecia** amphigenous, laterally compressed, 1–3 mm long, 1–5 mm high, yellow becoming paler, dehiscing irregularly; peridial cells 35–70 µm long, 16–34 µm wide, walls equally thickened (3–5 µm) or external wall thicker than internal, verrucose; spore mass orange-red. – **Primary aeciospores** globoid, ellipsoid, obovoid or angular, 20–40 × 16–27 µm; wall hyaline, 2–3 µm thick, densely verrucose; warts (ornaments) annulate and irregularly cylindrical with a flat top (Fig. 9b) in the majority of collections, rarely(?) tapering and with 'rootlike stilts' (see remarks below). – **Secondary aecia** (uredinia) hypophyllous, scattered, rounded or oblong, 0.4–0.7 mm in diam., soon naked, pulverulent, orange-red. – **Secondary aeciospores** (urediniospores) globoid, ellipsoid or ovoid, 20–40 × 16–25 µm; wall hyaline, 1–1.5 µm thick, densely and finely verrucose. – **Basidiosori** (telia) hypophyllous, rounded, scattered or confluent, forming waxy orange-red crusts, 0.4–0.8 mm in diam. – **Basidia** (teliospores) clavoid to cylindrical or ± prismatic, rounded at the apex, attenuate or rounded at the base, 60–105 × 15–24 µm; at first unicellular, then becoming 4-celled and greatly thickened and gelatinous at the apex; wall thin at the sides, 12–30 µm thick at the apex, hyaline, smooth. – Reference: Wilson and Henderson (1966: 3–4).

Remarks. Spermatogonia and primary aecia of this species complex are mainly found on the needles of *Pinus sylvestris*, *P. mugo* and *P. nigra* (but also on other two-needle pines, including cultivated species), secondary aecia and basidiosori chiefly on the leaves and stems of Asteraceae (especially trib. Senecioneae), Campanulaceae and Orobanchaceae trib. Pedicularieae. *Coleosporium* records on pines can only be assigned to one of our narrowly delimited species by inoculation experiments, by unambiguous field observations, or by molecular genetic evidence.

At least the European species of this complex are quite uniform morphologically, both in the aecial and in the telial stage. Blanz and Zwetko (2018: 300, fig. 4A) confirmed the occurrence of the second, apparently rare type of wall ornamentation of primary aeciospores in Austria (on *Pinus sylvestris* in Lower Austria), the tapering warts with 'rootlike stilts' which had already been described earlier (e.g., Holm et al. 1970: Plate I). However, in the majority of collections, warts were found to be irregularly cylindrical with a flat top (e.g., Helfer 2013; Blanz and Zwetko 2018: 300, fig. 4B).

Elongate secondary aeciospores and narrow basidia as well as the divergent host range in the dikaryotic stage (*Pulsatilla*, Ranunculaceae) support the separation of *Coleosporium pulsatillae* from *C. tussilaginis* s.l. (e.g., Kaneko 1981). Braun (1981) pointed out that the apical wall thickening of the basidia (teliospores) separates *C. inulae* (Fig. 13a) and *C. telekiae* from the complex. Beenken et al. (2017) confirm that molecular genetic evidence supports the separation of *C. pulsatillae* and *C. inulae* as distinct species (or species complexes, respectively). Cummins (1978) revised the N American taxa on Asteraceae and considered, i.a., the size of secondary aeciospores (urediniospores), basidia and basidiospores; two of the species accepted by Cummins (l.c.) also occur in Central Europe, *C. senecionis* and *C. sonchi*.

(2) *Coleosporium aposeridis* P. Syd. & Syd.

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* s. Braun (1981)

Life cycle insufficiently known:

(0,Ia on: *Pinus*?) – Klenke and Scholler (2015)

(Ib,III* on: *Aposeris foetida*)

Spermatogonia and primary aecia unknown. – **Secondary aecia** (uredinia) hypophyllous, in groups in leaf spots 2–4 mm wide, 0.2–0.4 mm in diam., golden-yellow, later fading. – **Secondary aeciospores** (urediniospores) polygonal-globose or polygonal-ellipsoidal, densely verrucose, 18–25 × 16–21 µm; wall hyaline, 1.5 µm thick. – **Basidiosori** (telia) hypophyllous, dispersed or irregularly grouped, 0.2–0.4 mm in diam., golden-yellow, more light-coloured later on. – **Basidia** (teliospores) cylindric-clavate, 60–80 × 15–18 µm, ± rounded at the apex; apical wall 15–25 µm thick. – Reference: Gäumann (1959: 118).

Remarks. Gäumann (1959) noted that the type location of this apparently rare rust is Carinthia, but it has been described from Slovenia (near Ljubljana/Laibach), not from Carinthia. Helfer (2013) lists *Aposeris foetida* as a host of *Coleosporium tussilaginis* f.sp. *sonchi* but does not mention *C. aposeridis* as a synonym (see below). According to Poelt and Zwetko (1997: 51–52), it has not been found in Austria so far.

3 *Coleosporium cacaliae* auct.

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* s. Braun (1981); ?*C. cacaliae* G.H. Otth; *C. tussilaginis* (Pers.) Lév. f.sp. *senecionis-silvatici* Boerema & Verh. (Helfer 2013); [non *Uredo cacaliae* DC. = *Coleosporium c.* (DC.) Rabenh. = *Uromyces c.* (DC.) Unger]

Heteropsis-form with secondary aecia:
(0,Ia on: *Pinus mugo*, *P. sylvestris*; inoculation experiments) – Gäumann (1959)
Ib,III* on: *Adenostyles alliariae*, *A. alpina* [syn. *A. glabra*], (*A. leucophylla*)

Spermatogonia and primary aecia not described in detail. – **Secondary aecia** (uredinia) hypophyllous, roundish, orange. – **Secondary aeciospores** (urediniospores) ellipsoidal, 24–35 × 21–24 µm; wall hyaline, thin, with small, stout, bacilliform warts. – **Basidiosori** (telia) hypophyllous, forming red wax-like crusts. – **Basidia** (teliospores) prismatic, 80–140 × 18–25 µm; apical wall thickened, up to 28 µm. – References: Gäumann (1959: 117), Klenke and Scholler (2015: 81).

Remarks. Apparently the name *Uredo cacaliae* DC. (now *Uromyces cacaliae*) has been misinterpreted for ages, and a correct name for the *Coleosporium* species on *Adenostyles* is still pending. Helfer (2013) includes *C. cacaliae* auct. with *C. tussilaginis* f.sp. *senecionis-sylvatici* (see below under *C. senecionis*). – For the distribution of *C. cacaliae* auct. in Austria see Poelt and Zwetko (1997: 52).

4 *Coleosporium campanulae* (Pers.) Tul.

Figs 10a, 11a, 12a

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* (Pers.) Lév. f.sp. *campanulae-rapunculoidis* Boerema & Verh. (Helfer 2013); *C. campanulacearum* Fr.; *C. phyteumatis* F. Wagner

Heteropsis-form with secondary aecia:
(0,Ia on: *Pinus sylvestris*, *P. mugo*, *P. nigra* and others; inoculation experiments) – Gäumann (1959)
Ib,III* on: *Campanula barbata*, *C. beckiana*, *C. bononiensis*, *C. carnica*, *C. cespitosa*, *C. cochleariifolia*, *C. glomerata*, *C. latifolia*, *C. moravica*, *C. patula*, *C. persicifolia*, *C. praesignis*, *C. rapunculoides*, *C. rapunculus*, *C. rotundifolia*, *C. scheuchzeri*, *C. trachelium*, *C. witasekiana*, *Legousia speculum-veneris*, *Lobelia cardinalis*, *Phyteuma betonicifolium*, *P. orbiculare*, *P. spicatum*, (*Campanula cervicaria*, *C. medium*, *C. pulla*, *C. rhomboidalis*, *C. sibirica*, *C. thyrsoides*, *Legousia hybrida*, *Phyteuma nigrum*)

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** (usually somewhat irregularly) elongate or ellipsoidal, 23–43 × 13–19 µm; wall hyaline, 3–4 µm thick, densely ornamented with warts 1–2 µm in diam., their central points 2–2.5 µm apart. – **Secondary aecia** (uredinia) hypophyllous, on some hosts also on stems, roundish or irregular, orange. – **Secondary aeciospores** (urediniospores) subglobose to oval, often slightly polygonal, 21–35 × 14–21 µm (after Gäumann 1959), (12.0–)20.5±4.8(–30.2) × (9.0–)14.9±3.2(–26.4) µm (after Helfer 2013); wall 1.5 µm thick, ornamented with fine warts 1 µm thick, their central points 1.5–2 µm apart. – **Basidiosori** (telia) at first yellowish-red, later blood-red, small but confluent to form larger crusts. – **Basidia** (teliospores) prismatic, 50–100 × 14–28 µm; apical wall 12–35 µm thick. – References: Gäumann (1959: 113–114), Helfer (2013: 91–92).

Remarks. Several taxa or 'biological forms' have been described within this taxon, from 'microspecies' (e.g., *Coleosporium campanulae-rapunculoidis* Kleb., *C. campanulae-trachelii* Kleb.) to formae speciales (e.g., Boerema and Verhoeven 1972). The host range of these taxa, however, appears to be quite irregular. Therefore, we assume that their taxonomic value might be questionable and prefer to unite them under the traditional name *C. campanulae*. Helfer (2013) united all those taxa under the name *C. tussilaginis* f.sp. *campanulae-rapunculoidis* Boerema & Verh. Another species growing on *Campanula*, *C. pseudocampanulae*, has been described from the Himalaya region by Kaneko et al. (1990). – For the distribution of *C. campanulae* in Austria see Poelt and Zwetko (1997: 52).

5 *Coleosporium cerinthes* J. Schröt. [nom. inval.]

Life cycle insufficiently known:
(0,Ia on: *Pinus*?) – Klenke and Scholler (2015)
Ib,III* on: *Cerinthe minor*

Spermatogonia and primary aecia unknown. – **Secondary aecia** (uredinia) hypophyllous, pulvinate to crust-like, small, orange-yellow. – **Secondary aeciospores** (urediniospores) 20–40 × 16–25 µm, densely and finely verrucose. – **Basidiosori** (telia) crustose, wax-like, small, orange-red. – **Basidia** (teliospores) palisade-like, conglutinate, 60–105 × 15–24 µm, apical wall 12–30 µm thick. – References: Schröter (1887: 370), Klenke and Scholler (2015: 275–276).

Remarks. This is an unresolved taxon of questionable status, described 'ad int[erim]' from scanty material collected in Silesia, Poland (Schröter 1887). Urban and Marková (2009) mention a record in their rust checklist of the Czech and Slovak Republics. The only collection from Austria (also on *Cerinthe minor*, herbarium C. B. Schiedermayr, LI) consists of a single leaf spot with a small group of sori and may just as well be interpreted as an incidental infection by another *Coleosporium* species (Poelt and Zwetko 1997: 52; Zwetko 2000: 11).

6 *Coleosporium doronici* Namysł.

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* s. Braun (1981); *C. tussilaginis* (Pers.) Lév. f.sp. *doronici* S. Helfer (Helfer 2013)

Heteropsis-form(?) with secondary aecia:
(0,Ia on: *Pinus mugo* agg.) – Klenke and Scholler (2015)
Ib,III* on: *Doronicum austriacum*, *D. glaciale* subsp. *calcareum* [syn. *D. calcareum*]

Figure 10. *Coleosporium* spp., secondary aecia (uredinia) and basidiosori (telia). **a1, a2.** *C. campanulae*, secondary aecia on *Campanula persicifolia*; **b1, b2.** *C. inulae*, secondary aecia on *Inula helenium*, basidiosori on *I. magnifica*; **c.** *C. pulsatillae*, secondary aecia on *Pulsatilla pratensis*; **d1, d2.** *C. senecionis*, basidiosori with germinated basidia on *Senecio ovatus* (recognisable by the somewhat pruinose surface), close-up with young basidiosori; (**b, c, d1** by Julia Kruse).

Spermatogonia and primary aecia unknown? – **Secondary aecia** (uredinia) hypophyllous, singly or in small groups, round, 0.3–0.5 mm in diam., golden yellow, later yellowish. – **Secondary aeciospores** (urediniospores) almost globose, less commonly ellipsoidal or ovoid, 22–32 × 17–27 µm (after Gäumann 1959), (10.8–)27.8±3.8(–34.1) × (7.0–)19.1±3.6(–24.8) µm (after Helfer 2013); wall hyaline, c. 1.5 µm thick, densely ornamented with coarse warts. – **Basidiosori** (telia) hypophyllous, dispersed or more commonly irregularly confluent, 0.4–0.7 µm in diam., golden yellow. – **Basidia** (teliospores) cylindric-clavate, 60–90 × 18–25 µm, rounded or narrowed at the base; apex rounded, apical wall 20–30 µm thick. – References: Gäumann (1959: 118), Helfer (2013: 92), Klenke and Scholler (2015: 352).

Remarks. Apparently this rarely recorded species prefers humid localities at montane to subalpine altitudes (Poelt and Zwetko 1997: 52–53).

7 *Coleosporium euphrasiae* (Schumach.) Fuss

Figs 11b, 12b

Syn. *Coleosporium tussilaginis* s.l.; *C. rhinanthacearum* (DC.) Fr.; *C. tussilaginis* (Pers.) Lév. f.sp. *rhinanthacearum* Boerema & Verh. (Helfer 2013); *Uredo rhinanthearum* Link

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus mugo*, *P. sylvestris*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Euphrasia officinalis*, *E. officinalis* subsp. *picta* [syn. *E. picta*], *E. officinalis* agg. [syn. *E. rostkoviana* agg.], *E. salisburgensis*, *E. stricta* agg., *Odontites vernus*?, *O. vulgaris* [syn. *O. ruber* p.p.], *O. vulgaris* agg. [*O. ruber* agg.], *Rhinanthus alectorolophus* agg., *R. aristatus* agg., *R. buccalis*, *R.* ×*digeneus*, *R. glacialis*, *R. minor*, *R. serotinus*, *R. serotinus* agg., (*Bartsia alpina*?, *Euphrasia hirtella*, *E. kerneri*, *E. micrantha*, *E. minima*, *E. nemorosa*, *E. nemorosa* × *stricta*, *Odontites luteus*, *Pedicularis palustris*, *Rhinanthus riphaeus* [syn. *R. pulcher*])

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** ± oval, often globose, rarely more elongate, 15–35 × 15–24 µm; wall 2–3 µm thick; warts 1–2 µm wide but sometimes confluent, their central points 2–3 µm apart. – **Secondary aecia** (uredinia) hypophyllous, 0.5 mm in diam., orange-yellow. – **Secondary aeciospores** (urediniospores) roundish or oval, rarely more elongate, partly polygonal, 18–29 × 13–18 µm (after Gäumann 1959), (19.2–)22.9±2.0(–28.4) × (14.1–)17.9±1.7(–22) µm (after Helfer 2013); wall c. 1 µm thick; warts c. 1 µm thick, their central points 1.5–2 µm apart. – **Basidiosori** (telia) mainly hypophyllous but also on stems and calyces, rather thick, wax-like, orange-red. – **Basidia** (teliospores) prismatic, 68–105 × 15–24 µm; apical wall 10–15 µm thick. – References: Gäumann (1959: 110), Helfer (2013: 94–95).

Remarks. The ultrastructure of the D-haustoria of *Coleosporium euphrasiae* is very characteristic and may distinguish this species from others (Berndt 1996). This rust is apparently widespread but locally uncommon. Because the 'telial' hosts are almost exclusively annual herbs of Orobanchaceae trib. Pedicularieae we may assume that its occurrence on these hosts is strictly dependent on host alternation. For the disputable nomenclature see Laundon (1975). – For the distribution of *C. euphrasiae* in Austria see Poelt and Zwetko (1997: 53).

8 *Coleosporium inulae* Rabenh.

Figs 10b, 11c, 12c, 13a

Syn. *Coleosporium tussilaginis* s.l. (s. Hylander et al. 1953 and others); *C. tussilaginis* (Pers.) Lév. f.sp. *inulae* S. Helfer (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Inula helenium*, *Pentanema ensifolium* [syn. *Inula ensifolia*], *P. salicinum* [syn. *I. salicina*], (*P. germanicum* [syn. *I. germanica*])

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** mainly elongate, only few subglobose or oval, 20–40 × 13–18 µm; wall hyaline, 3–3.5 µm thick, densely verrucose; warts 1–2 µm thick, their central points 2–2.5 µm apart. – **Secondary aecia** (uredinia) hypophyllous, causing small yellowish leaf spots, up to 0.5 mm in diam., bright orange-yellow. – **Secondary aeciospores** (urediniospores) usually elongate-oval or elongate, rarely ± globose, often somewhat polygonal, 19–30 × 12–15 µm (after Gäumann 1959), (21.2–)30.3±3.3(–39.5) × (15.7–)23.4±3.1(–30.7) µm (after Helfer 2013); wall hyaline, c. 1.5 µm thick; warts c. 1 µm wide, their central points 1–1.5 µm apart. – **Basidiosori** (telia) hypophyllous, forming small crusts up to 1 mm in diam., at first yellow, later red. – **Basidia** (teliospores) prismatic, 90–110 × 16–22 µm; apical wall 35–40 µm thick. – References: Gäumann (1959: 119–120), Helfer (2013: 92–93).

Remarks. Braun (1981) has drawn attention to the conspicuously thickened apical wall of the basidia (teliospores), a useful diagnostic character. Beenken et al. (2017) confirm that also molecular genetic evidence clearly supports the separation of *Coleosporium inulae* as a distinct species. – For records of *C. inulae* in Austria see Poelt and Zwetko (1997: 53).

(9) *Coleosporium ligulariae* Thüm.

Syn. *Coleosporium tussilaginis* s.l.; *C. inulae* Rabenh. s. Braun (1981); *C. tussilaginis* (Pers.) Lév. f.sp. *senecionis-silvatici* Boerema & Verh. (Helfer 2013)

Life cycle insufficiently known:

(0,Ia on: *Pinus*?) – Klenke and Scholler (2015)

(Ib,III* on: *Ligularia sibirica*)

Spermatogonia and primary aecia unknown. – **Secondary aecia** (uredinia) hypophyllous, orange, 0.5 mm in

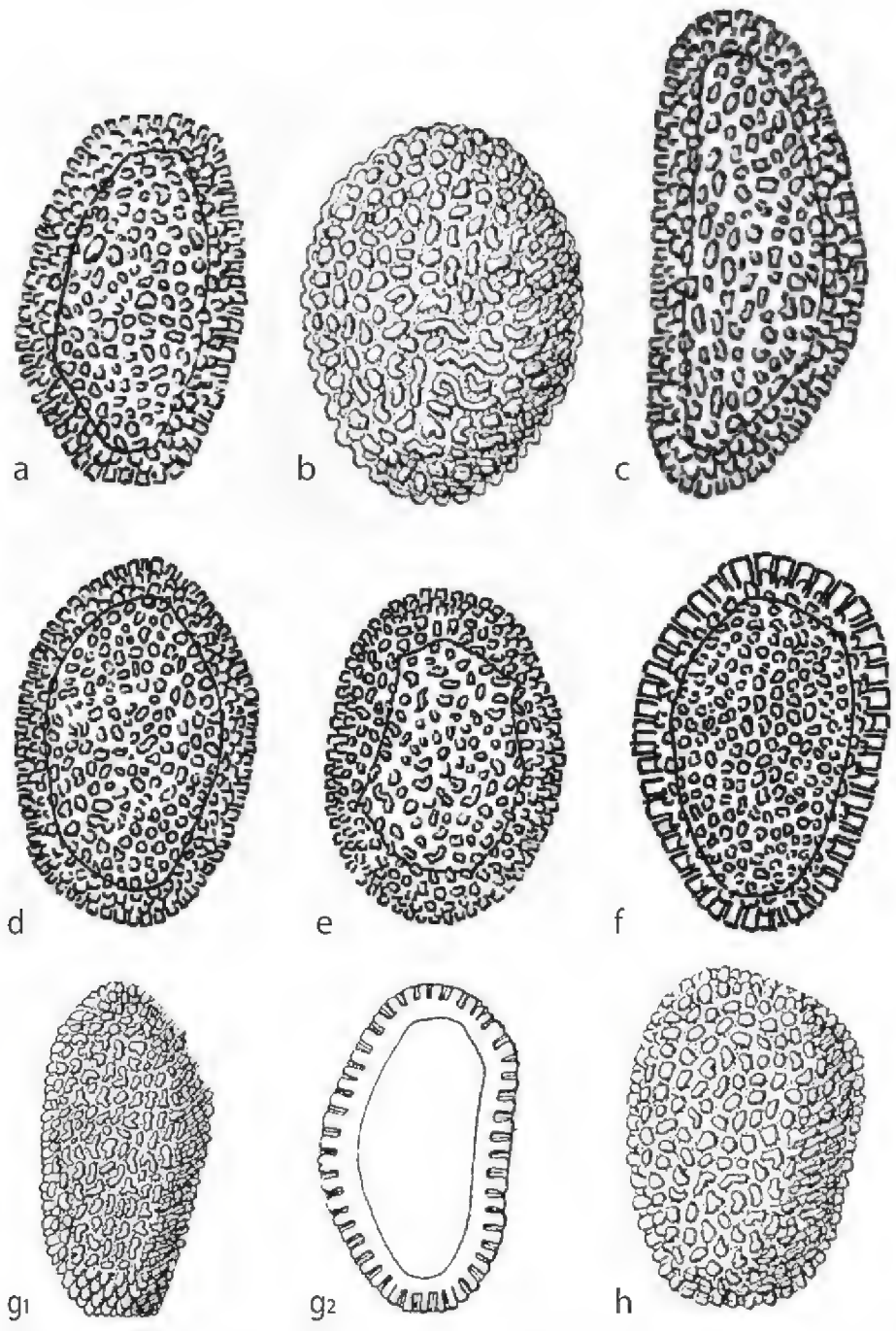


Figure 11. *Coleosporium* spp., primary aeciospores from aecia on *Pinus sylvestris*: **a.** *C. campanulae*; **b.** *C. euphrasiae*; **c.** *C. inulae*; **d.** *C. melampyri*; **e.** *C. pulsatillae*; **f.** *C. sonchi*; **g1, g2.** *C. senecionis*, in surface view and optical section; **h.** *C. tussilaginis*; (**a–h** from Klebahn 1914: 722, 746).

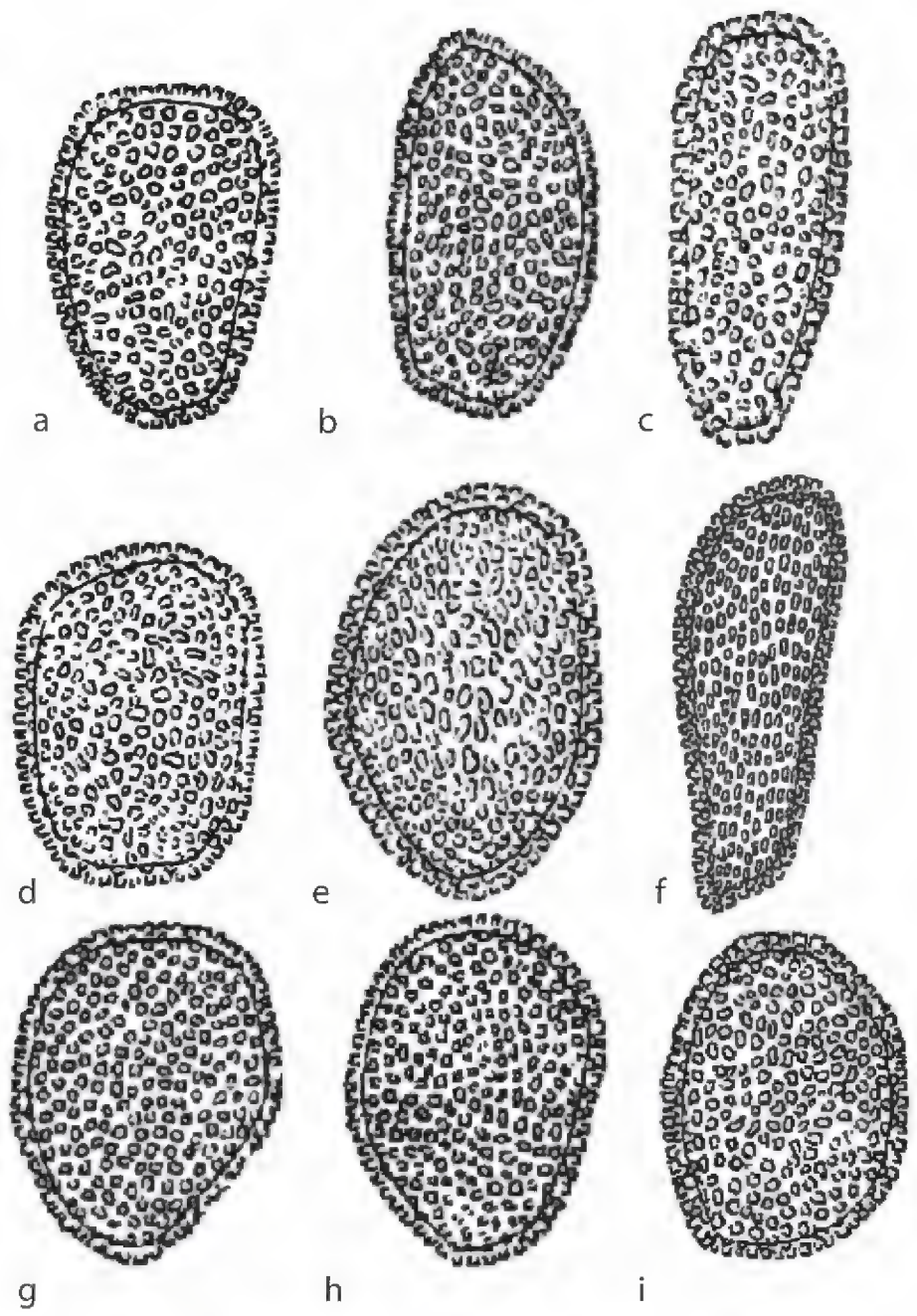


Figure 12. *Coleosporium* spp., secondary aeciospores (urediniospores): **a.** *C. campanulae* on *Campanula rapunculoides*; **b.** *C. euphrasiae* on *Rhinanthus minor*; **c.** *C. inulae* on *Pentanema salicinum* (syn. *Inula salicina*); **d.** *C. melampyri* on *Melampyrum pratense* agg.; **e.** *C. petasitis* on *Petasites hybridus*; **f.** *C. pulsatillae* on *Pulsatilla vulgaris*; **g.** *C. senecionis* on *Senecio sylvaticus*; **h.** *C. sonchi* on *Sonchus arvensis*; **i.** *C. tussilaginis* on *Tussilago farfara*; (**a–i** from Klebahn 1914: 722, 746).

diam. – **Secondary aeciospores** (urediniospores) 21–36 × 16–26 µm, verrucose. – **Basidiosori** (telia) red, densely grouped, forming wax-like crusts. – **Basidia** (teliospores) palisade-like, conglutinate, 70–110 × 19–28 µm; apical wall 25–40 µm thick. – References: Azbukina (1974: 182), Kuprevič and Uljaniščev (1975: 115–116), Klenke and Scholler (2015: 515).

Remarks. Hylander et al. (1953) treated *Coleosporium ligulariae* as a synonym of *C. senecionis* (DC.) Kickx, and the latter as a race of *C. tussilaginis* s.l. Similarly, Helfer (2013) includes *C. ligulariae* with *C. tussilaginis* f.sp. *senecionis-sylvatici* (see below under *C. senecionis*). In Europe, *C. ligulariae* is reported on cultivated *Ligularia* species from botanical gardens (e.g., Hylander et al. 1953). Poelt and Zwetko (1997) do not mention *C. ligulariae*, but this rust species is widespread in Siberia and its natural range reaches Europe in Finland and Romania (Gäumann 1959).

10 *Coleosporium melampyri* (Rebent.) Tul.

Figs 11d, 12d, 13b

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* (Pers.) Lév. f.sp. *melampyri* Boerema & Verh. (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*, *P. mugo*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Melampyrum arvense* agg., *M. nemorosum*, *M. nemorosum* agg., *M. pratense* agg., *M. sylvaticum* agg., (*M. cristatum*)

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** usually oval, more rarely subglobose or elongate, 22–35 × 17–24 µm; wall 3–4 µm thick; warts 1–2 µm wide, their central points 1.5–2 µm apart. – **Secondary aecia** (uredinia) hypophyllous, orange-yellow, c. 0.5 mm in diam. – **Secondary aeciospores** (urediniospores) subglobose, oval or elongate, often somewhat polygonal, 14–35 × 12–28 µm (after Gäumann 1959), (20.6–)25.9±2.6(–32.4) × (13.3–)18.9±2.2(–24.2) µm (after Helfer 2013); wall hyaline, thin; warts c. 1.5 µm thick, their central points 1.5–2 µm apart. – **Basidiosori** (telia) hypophyllous, occasionally in groups, wax-like, red. – **Basidia** (teliospores) prismatic, 70–115 × 14–28 µm; apical wall

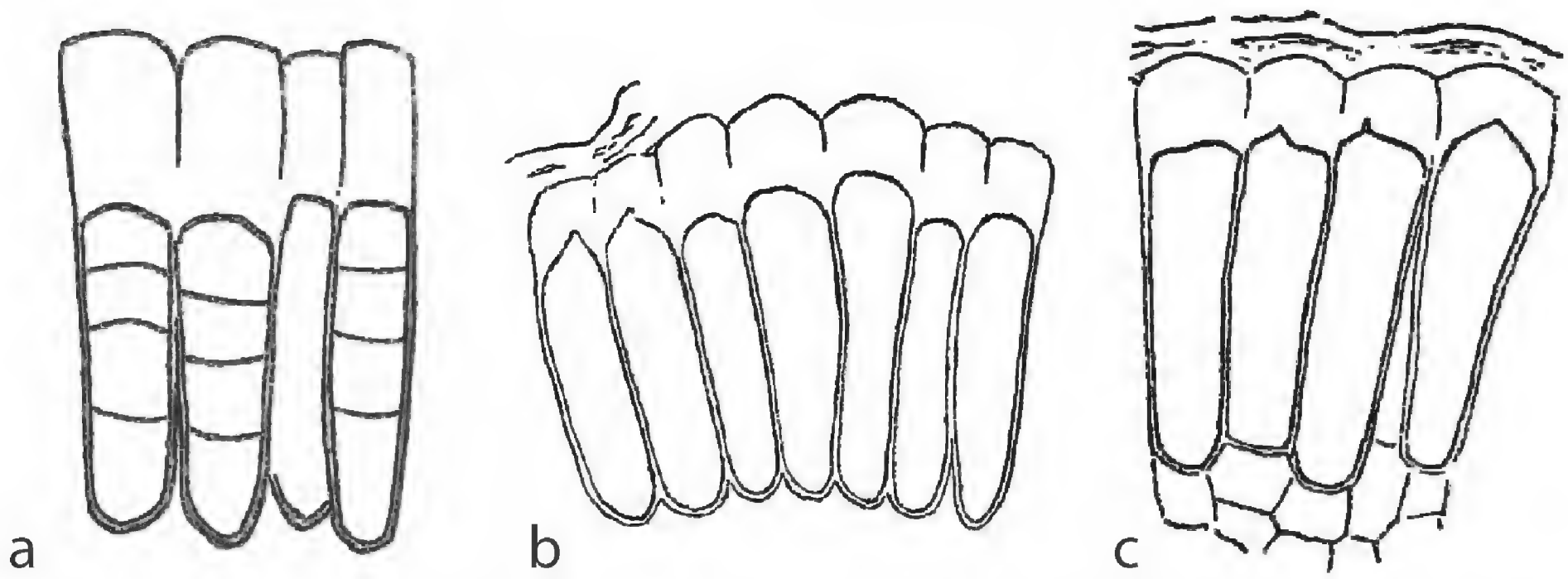


Figure 13. *Coleosporium* spp., basidia (teliospores): **a.** *C. inulae* on *Pentanema salicinum* (syn. *Inula salicina*), basidia with conspicuously thickened apical wall; **b.** *C. melampyri* on *Melampyrum pratense* agg.; **c.** *C. senecionis* on *Senecio sylvaticus*; (**a–c** from Klebahn 1914: 746).

10–28 µm thick. – References: Gäumann (1959: 112), Helfer (2013: 93).

Remarks. As the 'telial' hosts are annual herbs we may assume that the occurrence of *Coleosporium melampyri* on these hosts is dependent on host alternation. – For the distribution of *C. melampyri* in Austria see Poelt and Zwetko (1997: 53).

11 *Coleosporium petasitis* (DC.) Berk.

Fig. 12e

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* U. Braun (1981); *C. petasitidis* (DC.) Thüm. (orthogr. var.); *C. tussilaginis* (Pers.) Lév. f.sp. *petasitis* Boerema & Verh. (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Petasites albus*, *P. hybridus*, *P. paradoxus*

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Secondary aecia** (uredinia) hypophyllous, orange, c. 0.5 mm in diam. – **Secondary aeciospores** (urediniospores) ellipsoid or ovoid, 21–32(–42) × 14–21 µm (after Gäumann 1959), (18.4–)26±2.3(–31.6) × (14.3–)20.7±2.2(–26.6) µm (after Helfer 2013); wall 1.5 µm thick, hyaline; warts short-bacilliform, up to 1.25 µm thick, their central points c. 1.5 µm apart. – **Basidiosori** (telia) forming small red crusts c. 0.5 mm in diam., in groups or confluent. – **Basidia** (teliospores) prismatic, 60–100 × 14–24 µm, apical wall 17–20 µm thick. – References: Gäumann (1959: 121), Helfer (2013: 93–94).

Remarks. According to Klenke and Scholler (2015), *Coleosporium petasitis* is common in the montane to subalpine belt. Therefore, we presume that primary aecia could also be found on *Pinus mugo*. – For the distribution of *C. petasitis* in Austria see Poelt and Zwetko (1997: 53–54).

12 *Coleosporium pulsatillae* (F. Strauss) Lév.

Figs 10c, 11e, 12f, 14

Syn. *Coleosporium tussilaginis* s.l. (s. Hylander et al. 1953 and others); *C. tussilaginis* (Pers.) Lév. f.sp. *pulsatillae* Boerema & Verh. (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Pulsatilla grandis*, *P. oenipontana*, *P. pratensis* subsp. *nigricans*, *P. styriaca*, *P. vulgaris*, (*P. alpina*, *P. vernalis*)

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** usually irregular-oval, 25–40 × 16–24 µm; wall 3.5–4.5 µm thick, with small thinner spots; warts c. 1 µm in diam. – **Secondary aecia** (uredinia) hypophyllous, bright yellow-orange, 0.5–1 mm in diam., surrounded by remnants of the ruptured epidermis. – **Secondary aeciospores** (urediniospores) usually oblong or clavate, somewhat blunt-polygonal, occasionally irregularly ellipsoidal or oval, 18–50 × 10–15 µm (Gäumann 1959), (20.8–)28.7±4.2(–40.3) × (15.5–)19.6±2.2(–24.4) µm (Helfer 2013); wall thin, ≥1 µm, covered with fine warts. – **Basidiosori** (telia) hypophyllous, blood-red, forming cushion-like crusts covered by the epidermis, c. 0.5 mm in diam. – **Basidia** (teliospores) cylindrical-prismatic, 65–100 × 10–22 µm; lateral walls thin, apical wall ≤ 15 µm thick. – **Basidiospores** c. 8 µm. – References: Gäumann (1959: 108–110), Helfer (2013: 94).

Remarks. This is a well separated, distinctive *Coleosporium* species, the only one on a genus of Ranunculaceae in Europe; see Beenken et al. (2017) for molecular phylogenetic data. Due to its peculiar host range and a few morphological characters, it has been separated from the traditional '*C. tussilaginis* s.l.' before (e.g., Kaneko 1981). The basidia and the secondary aeciospores are narrower in proportion than those of other *Coleosporium* species in Central Europe, but the measurements seem quite divergent in the literature (see above). More

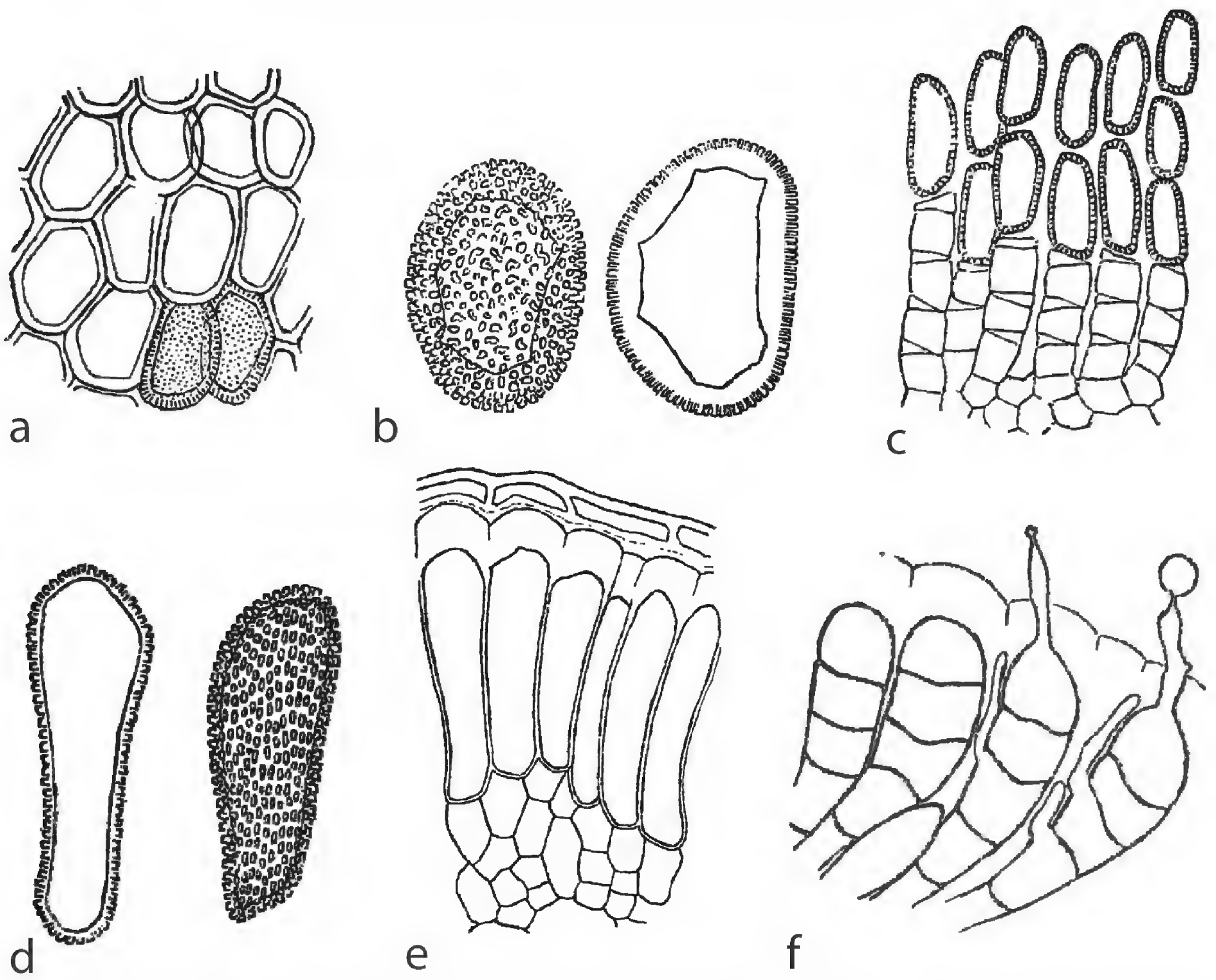


Figure 14. *Coleosporium pulsatillae*. **a, b.** On *Pinus sylvestris*: **a.** Peridium cells of primary aecium in surface view; **b.** Primary aeciospores in combined view and optical section; **c–f.** On *Pulsatilla vulgaris*: **c.** Chains of secondary aeciospores (urediniospores); **d.** Secondary aeciospores; **e.** Basidiosorus (telium) in vertical section; **f.** Germinating basidia; (**a–f** from Klebahn 1914: 746).

Coleosporium species on Ranunculaceae are known from Asia. – For records of *C. pulsatillae* in Austria see Poelt and Zwetko (1997: 54).

13 *Coleosporium senecionis* (Schumach.) Fr.

Figs 10d, 11g, 12g, 13c

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* s. Braun (1981); *C. senecionis* (Pers.) Lév. f.sp. *senecionis-silvatici* Wagner ex Gäum.; *C. tussilaginis* f.sp. *senecionis-silvatici* Boerema & Verh. (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*, *P. mugo*, *P. nigra*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Senecio cordatus*, *S. doria* agg., *S. germanicus*, *S. hercynicus*, *S. jacobaea*, *S. nemorensis* agg., *S. ovatus*, *S. rupestris*, *S. sarracenicus*, *S. subalpinus*, *S. sylvaticus*, *S. umbrosus*, *S. viscosus*, *S. vulgaris*, *Tephroseris longifolia*, (*Calendula officinalis*?, *Pericallis cruenta* cv. [syn. *Senecio cruentus*], *S. doria*, *S. doronicum*, *S. erucifolius*, *S. paludosus*, *S. vernalis*)

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** either oval or elongate-oval to elongate, only few subglobose, 20–50 × 15–25 µm; wall 3–4 µm thick, coarsely verrucose; warts 1–2 µm thick, their central points 2–2.5 µm apart. – **Secondary aecia** (uredinia) hypophyllous, rarely epiphyllous, often on stems, up to 1 mm in size, bright yellow-orange. – **Secondary aeciospores** (urediniospores) in short chains, bright yellow-orange, mostly elongate or oval, (17–)22–27(–34) × (14–)18–22(–27) µm, mean 25 × 21.5 µm (after Gäumann 1959); wall 1–2 µm thick, finely verrucose; warts c. 1.5 µm apart. – **Basidiosori** (telia) hypophyllous and on stems, up to 1 mm in size, often in large groups and ± confluent, forming red cushions or crusts. – **Basidia** (teliospores) prismatic, up to 100 × 18–24 µm; apical wall up to 22 µm thick. – References: Gäumann (1959: 122), Helfer (2013: 95).

Remarks. Helfer (2013) treats this taxon under *Coleosporium tussilaginis* f.sp. *senecionis-silvatici* Boerema & Verh. and includes *C. cacaliae* auct. and *C. ligulariae*. However, his measurements of secondary aeciospores (urediniospores) are very similar,

(18.6–)25.7±3.2(–37.1) × (11.8–)18.7±2.2(–26.4) µm. Further *Coleosporium* species on *Senecio* have been recorded in Asia (e.g., Kaneko 1981; Kaneko et al. 1990). – For numerous records of *C. senecionis* in Austria see Poelt and Zwetko (1997: 54).

According to Klenke and Scholler (2015), the *Coleosporium* on *Calendula officinalis* should be separated as ***C. calendulae*** Speg., a species rarely recorded in Germany (secondary aeciospores mostly 22–27 × 18–22 µm, finely verrucose). Helfer (2013) did not mention this taxon.

14 *Coleosporium sonchi* (F. Strauss) Lév. [nom. inval.]

Figs 11f, 12h

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* s. Braun (1981); *C. tussilaginis* (Pers.) Lév. f.sp. *sonchi* Boerema & Verh. (Helfer 2013); *C. sonchi* (Schumach.) Lév. ex Tul.

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Emilia sonchifolia* cult., *Sonchus arvensis*, *S. arvensis* subsp. *uliginosus*, *S. asper*, *S. oleraceus*, (*Crepis tectorum*, *Lapsana communis*, *Lactuca muralis* [syn. *Mycelis m.*], *Sonchus palustris*)

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** short-ellipsoidal to blunt-polyhedral, 25–32 × 18–25 µm; wall hyaline, 2–3 µm thick, coarsely verrucose, central points of the warts 2–2.5 µm apart. – **Secondary aecia** (uredinia) hypophyllous, c. 0.5 mm in diam., bright yellow-orange. – **Secondary aeciospores** (urediniospores) 18–27 × 14–20 µm µm (after Gäumann 1959), (15.9–)21.8±2.5(–29.6) × (9.6–)17.2±3.0(–23.9) µm (after Helfer 2013); wall 1–1.5 µm thick; warts c. 1 µm thick, their central points 1–1.5 µm apart. – **Basidiosori** (telia) forming small flat red crusts, often in large groups. – **Basidia** (teliospores) prismatic, 60–100 × 13–24 µm; apical wall 15–20 µm thick. – References: Gäumann (1959: 126), Helfer (2013: 96).

Remarks. Helfer (2013) treats this taxon under *Coleosporium tussilaginis* f.sp. *sonchi* Boerema & Verh., a form restricted to Asteraceae trib. Cichorieae. He also lists *Aposeris foetida* as a host of this forma specialis, but does not mention *C. aposeridis* as a synonym. – For records of *C. sonchi* in Austria see Poelt and Zwetko (1997: 54–55).

15 *Coleosporium telekiae* Thüm.

Syn. *Coleosporium tussilaginis* s.l.; *C. tussilaginis* (Pers.) Lév. f.sp. *telekiae* S. Helfer (Helfer 2013)

Life cycle insufficiently known:

(0,I on: *Pinus*?) – Klenke and Scholler (2015)

Ib,III* on: *Telekia speciosa*

Spermatogonia and primary aecia unknown. – **Secondary aecia** (uredinia) hypophyllous, in yellowish or brown spots, dispersed or in irregular groups, 0.3–0.6 mm in diam., golden-yellow, later pallid. – **Secondary aeciospores** (urediniospores) subglobose to ellipsoidal, ovoid or elongate 18–28 × 16–22 µm (after Gäumann 1959), (15.8–)22.6±3.0(–31.8) × (10.6–)17.2±2.4(–24.1) µm (after Helfer 2013); wall hyaline, 1–1.5 µm thick, densely verrucose. – **Basidiosori** (telia) hypophyllous, dispersed or in irregular groups, ± circular, 0.4–0.6 mm in diam., golden yellow, later pale yellowish. – **Basidia** (teliospores) cylindrical or slightly clavate, 80–130 × 19–25 µm; apex rounded, apical wall 25–35 µm thick. – References: Gäumann (1959: 127), Helfer (2013: 96).

Remarks. The host plant of *Coleosporium telekiae*, *Telekia speciosa*, has been introduced from E Central Europe and is now locally naturalised. – For records of *C. telekiae* in Austria see Poelt and Zwetko (1997: 55).

16 *Coleosporium tussilaginis* (Pers.) Tul. s.str.

Figs 11h, 12i, 15

Syn. *Coleosporium tussilaginis* (Pers.) Lév. f.sp. *tussilaginis* (Helfer 2013)

Heteropsis-form with secondary aecia:

(0,Ia on: *Pinus sylvestris*, *P. mugo*, *P. nigra* and others; inoculation experiments) – Gäumann (1959)

Ib,III* on: *Tussilago farfara*

Spermatogonia and **primary aecia** see above under *C. tussilaginis* s.l. – **Primary aeciospores** mostly oval, sometimes subglobose, less commonly elongate, 15–24(–35) × 15–24 µm; wall 2–2.5 µm thick, warts 1–1.5 µm thick, their central points 2–2.5 µm apart. – **Secondary aecia** (uredinia) hypophyllous, up to 0.5 mm in diam., in dispersed or ± aggregated groups, bright orange-yellow. – **Secondary aeciospores** (urediniospores) mostly oval, also subglobose or somewhat elongate or irregular, 22–32 × 15–22 µm (Gäumann 1959), (21.7–)28.3±3.2(–39.6) × (15.9–)20.8±2.4(–26.6) µm (Helfer 2013); wall c. 1.5 µm thick, evenly coarsely verrucose; warts >1 µm thick, their central points c. 1.5 µm apart. – **Basidiosori** (telia) hypophyllous, red, filling the intercellular spaces in the mesophyll, small but ± confluent and sometimes covering the whole lower leaf surface. – **Basidia** (teliospores) prismatic, 60–140 × 15–28 mm, apical wall 10–21 µm thick. – References: Gäumann (1959: 128–129), Helfer (2013: 90–91).

Remarks. This is presumably the most commonly recorded *Coleosporium* species in Austria (Poelt and Zwetko 1997: 55).

Cronartium Fr.

Syn. *Endocronartium* Y. Hirats.; *Peridermium* (Link) J.C. Schmidt & Kunze p.p.

N.B.: In contrast to the original manuscript, the anamorph genus *Peridermium* is now included in this genus. The corresponding passages concerning *Peridermium* and *Peridermium pini* (*Cronartium p.*) have been re-arranged and inserted here.

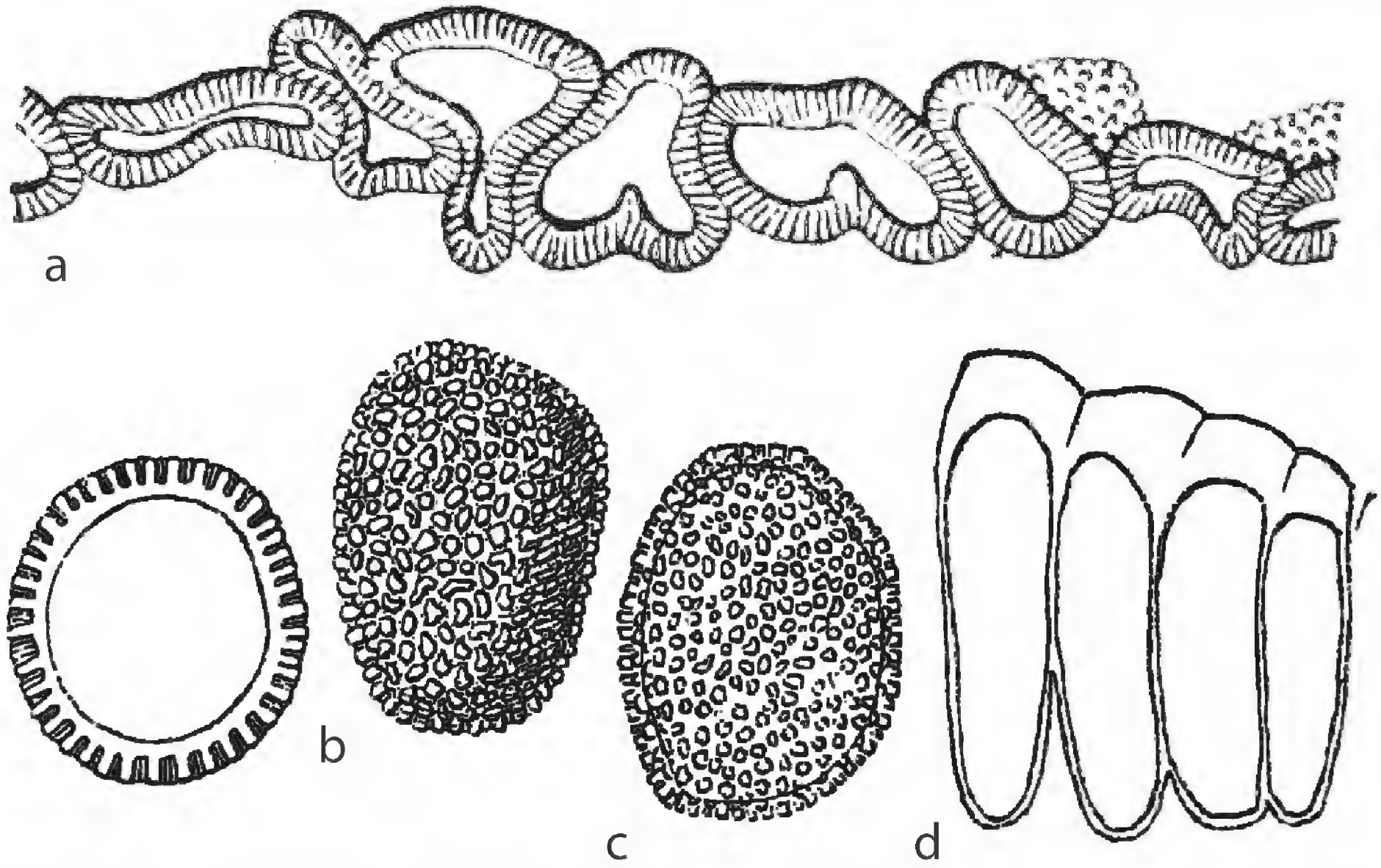


Figure 15. *Coleosporium tussilaginis* s.str. **a, b.** On *Pinus sylvestris*: **a.** Peridium cells of primary aecium in longitudinal section; **b.** Primary aeciospores in optical section and surface view; **c, d.** On *Tussilago farfara*: **c.** Secondary aeciospore (urediniospore); **d.** Basidia (teliospores); (**a–d** from Klebahn 1914: 746).

Cronartium is a genus with some representatives of economic importance, and two of them have been confirmed from Austria. – Diagnosis (e.g., Brandenburger 1985: 1028): **Spermatogonia** subepidermal, intracortical. – **Aecia** peridermioid, at first intraepidermal, later erumpent. – **Aeciospores** formed in chains with intercalary cells. – **Uredinia** subepidermal; peridium opening with an apical pore. – **Urediniospores** stipitate, formed singly. – **Telia** subepidermal (originating from empty uredinia), column-like, consisting of long, conglutinate chains of 1-celled teliospores. – **Teliospores** germinate readily with 4-celled phragmobasidia.

The name *Peridermium* has been widely used for aecial states of *Cronartium*, but also for those of other teleomorphic genera producing peridermioid aecia on conifers (e.g., *Chrysomyxa*, *Coleosporium*, *Pucciniastrum* s.l.). Some autoecious, reportedly endocyclic *Peridermium* (*Cronartium*) taxa have been placed in the genus *Endocronartium* Y. Hirats. (e.g., Hiratsuka 1969), but this genus has not been broadly accepted. For instance, already Vogler and Bruns (1993) stated that accumulating molecular genetic evidence suggested that the *Endocronartium* species described by Hiratsuka (l.c.) belong in three separate *Cronartium* clades, making *Endocronartium* polyphyletic. Vogler and Bruns (1993: 245) concluded that "Placing rusts with divergent phylogenetic lineages into a single polyphyletic genus solely on the basis of nuclear behavior, …, is not phylogenetically advisable". Moreover, the observations of Hiratsuka et al. (1966) on nuclear behaviour in aeciospores and their germ tubes in *Peridermium harknessii* J.P. Moore (the type of *Endocronartium*) were doubted by several authors. However, recent results of molecular genetic studies (Samils et al. 2021) confirm the existence of autoecious, possibly anamorphic (asexual) entities cautiously named 'life cycle forms', but not necessarily endocyclic *Cronartium* species. For details see below under *Cronartium pini*.

1 *Cronartium flaccidum* (Alb. & Schwein.) G. Winter

Figs 16, 17

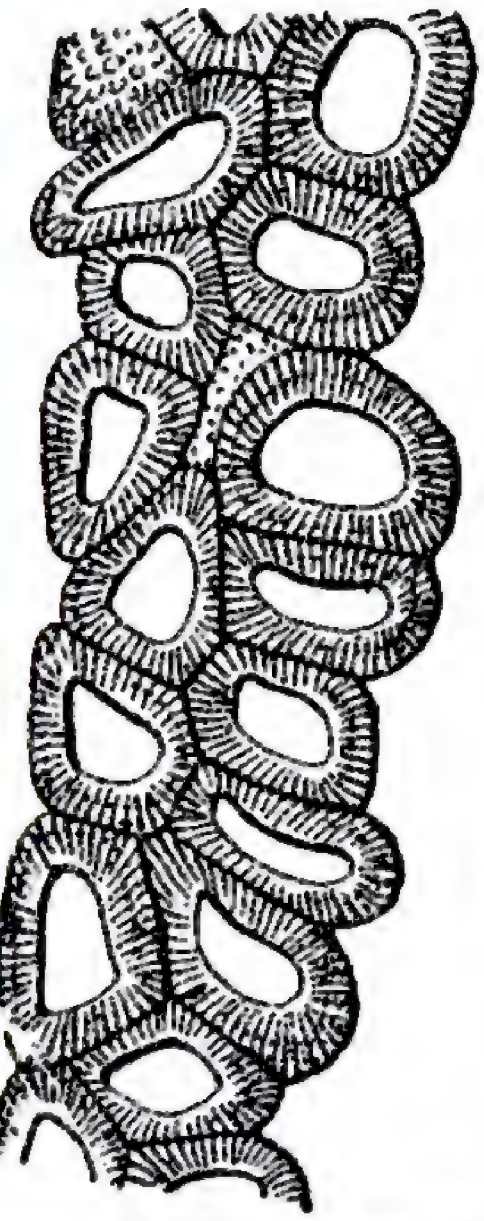
Syn. *Cronartium asclepiadeum* (Willd.) Fr.; *C. gentianeum* Thüm.; *C. paeoniae* Castagne; *Peridermium cornui* Rostr. emend. Kleb.; *Cronartium pini* s.l.; *Peridermium pini* s.l.

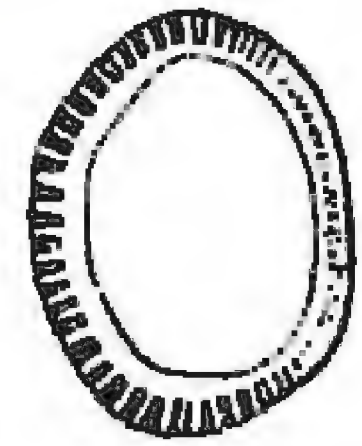
Hetereu-form:

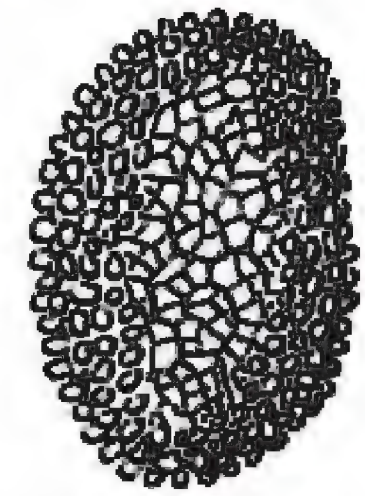
0,I on: *Pinus mugo*, *P. sylvestris*, (*P. uliginosa* [syn. *P. ×rotundata*], *P. uncinata*)

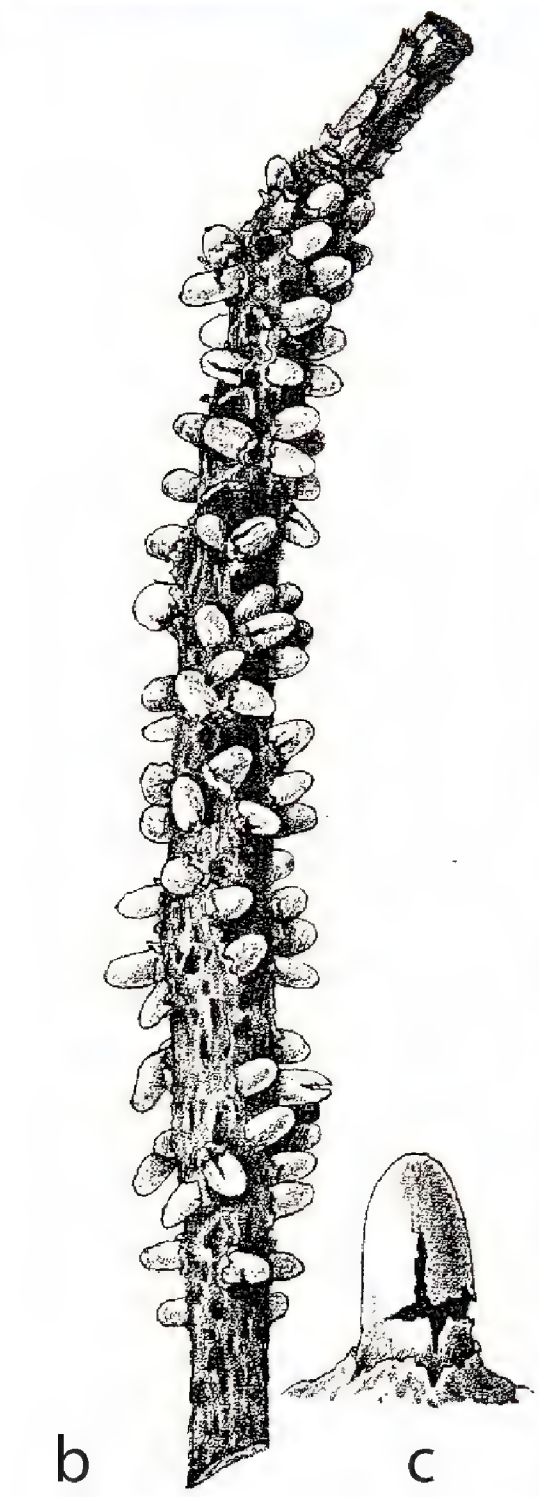
II,III on: *Gentiana asclepiadea*, *Impatiens balsamina* cult., *Paeonia* sp. cult., *Tropaeolum* sp. cult., *Vincetoxicum hirundinaria*, (*Asclepias syriaca*, *Melampyrum cristatum*, *M. arvense* agg., *M. sylvaticum* agg., *Myosotis laxa*, *Pedicularis palustris*, *P. sceptrum-carolinum*)

Spermatogonia intracortical. – **Aecia** erumpent from the cortex, usually in large groups clasping around the whole branch or stem; peridium inflated, 2–8 mm long, 2–3 mm wide and 2–3 mm high, mostly of 2 cell layers. – **Aeciospores** subglobose-ellipsoidal or slight-









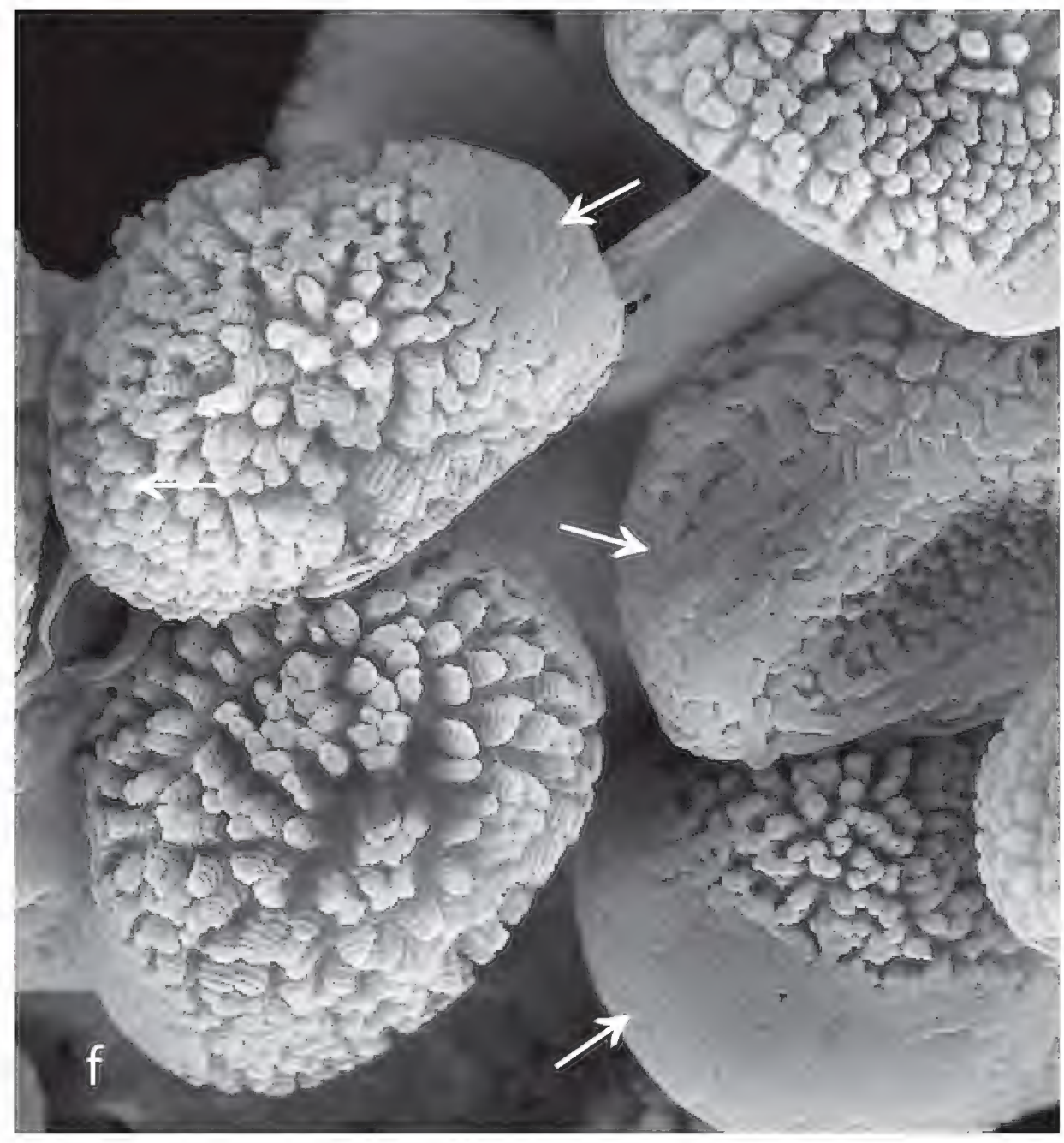


Figure 16. *Cronartium flaccidum* f.sp. *flaccidum* on *Pinus sylvestris*: **a.** Stem of young tree with numerous aecia; **b.** Slightly swollen *Pinus* twig with aecia; **c.** Mature aecium with rupturing peridium; **d.** Peridium cells in longitudinal section; **e.** Aeciospores in optical section and surface view; note the reticulate cracks in the smooth part of the spore wall; **f.** Aeciospores in SEM showing the broad, nearly smooth part of the spore wall with the fine network of cracks (arrows) and the annulate wall ornaments; (**a** by Julia Kruse; **b, c** from Dietel 1928: 42, with permission from Duncker & Humblot GmbH; **d, e** from Klebahn 1914: 722; **f** from Zwetko and Blanz 2018: 277).

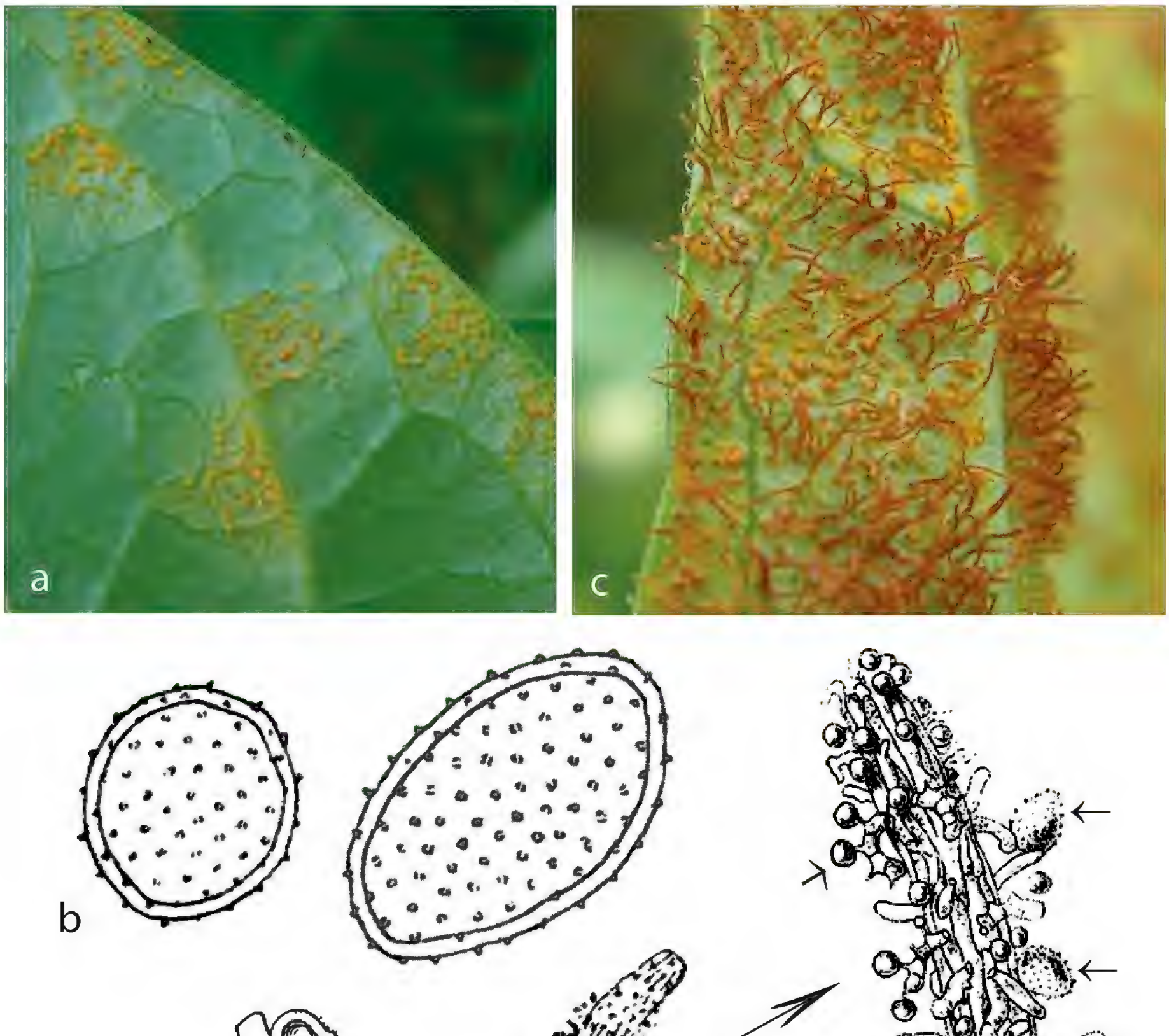


Figure 17. *Cronartium flaccidum* f.sp. *flaccidum* on *Vincetoxicum hirundinaria*: **a.** Uredinia; **b.** Urediniospores; **c.** Teliospore columns (telia); **d.** Telium consisting of an erumpent long column of strongly coherent teliospores; **e.** Teliospore column with germinated teliospores bearing curved phragmobasidia with basidiospores (arrowhead); urediniospores adhering to the column (arrows) indicate that the telia emerge from uredinia, as well as (**f**) the uredinial peridium under the host epidermis around the base of the teliospore column; (**a, c** by Julia Kruse; **b, d, f** from Klebahn 1914: 722; **e** from Dietel 1928: 43, after Tulasne, with permission from Duncker & Humblot GmbH).

ly polyhedral, 22–26(–30) × 16–20 µm; wall hyaline, verrucose but with a nearly smooth strip showing only a network of fine furrows; warts bacilliform (annulate in SEM), their central points 1.5–2 µm apart; verrucose wall area 3–4 µm thick, smooth area 2–3 µm. – **Uredinia** hypophyllous, evenly dispersed in yellow leaf spots, up to 0.25 mm in diam., pustule-like, opening with an apical pore. – **Urediniospores** ovate or ellipsoidal, 21–27 × 15–20 µm; wall hyaline, 1.5–2 µm thick; warts acute, 2.5–4 µm apart. – **Telia** (teliospore columns) in groups or rarely evenly dispersed over the whole leaf surface, yellow-brown or brown, horn-like when dry, 1–2 mm long, 60–130 µm thick. – **Teliospores** ellipsoidal or elongate, 26–56 × 9–14 µm, with thin walls. – **Basidiospores** subglobose, c. 8 µm in diam. – Reference: Gäumann (1959: 81).

Remarks. Two formae speciales are separated by their main host species in the telial stage, ***Cronartium flaccidum*** f.sp. ***flaccidum*** on *Vincetoxicum hirundinaria* and f.sp. ***gentianeum*** on *Gentiana asclepiadea*. Both forms, however, are able to infect quite a number of unrelated dicotyledons, a highly divergent feature in rust fungi. – For the distribution of both f.sp. in Austria see Poelt and Zwetko (1997: 57–58).

Klebahn (1914) observed that in *Cronartium ribicola* the aeciospore wall is thicker on the smooth side (3–3.5 µm) than on the verrucose side (2–2.5 µm), whereas in *C. flaccidum* the verrucose side has a thicker wall (3–4 µm) than the nearly smooth side (2–3 µm). According to Klebahn's interpretation, the smooth strip on the aeciospore surface of *C. ribicola* is produced by fusion of warts, whereas in *C. flaccidum* the warts on the nearly smooth strip are distinctly broader with narrow spacing visible as a network of fine furrows.

2 *Cronartium pini* (Willd.) Jørst. s.str.

Syn. *Aecidium pini* (Willd.) Pers. ex J.F. Gmel.; *Peridermium pini* (Willd.) J.C. Schmidt & Kunze s.str.; *Endocronartium pini* (Willd.) Y. Hirats.

Life cycle insufficiently known (anamorphic taxon or endo-form?):

0,I on: *Pinus nigra*?, *P. sylvestris*?, (*P. mugo*)

Spermatogonia and **aecia** as in *Cronartium flaccidum*.

Remarks. The name *Peridermium pini* (or *Cronartium pini*, respectively) has been used for both the aecial stage of *Cronartium flaccidum* and for a closely related, morphologically indistinguishable pine-to-pine rust. Already Klebahn (1890a) divided *Peridermium pini* into two species: *P. pini* (Willd.) Lév. emend. Kleb. and *P. cornui* Rostr. emend. Kleb. The latter was recognised as the anamorph of the heteroecious rust *C. flaccidum*, the former was frequently found on sites where the known telial host of *C. flaccidum* was rare or absent. The first successful infection experiments with pine-to-pine forms of *Peridermium pini* have been reported by Haack (1914). The only infectious spores known from *P. pini* (and similar autoecious pine rusts) are aeciospores, which again infect pines.

Hiratsuka et al. (1966) observed that young, immature aeciospores of *Peridermium harknessii* J.P. Moore (*Endocronartium h.*, ?*Cronartium quercuum*) have two nuclei and that mature spores have only one. In the developing germ tubes, they found two, three or four nuclei. They concluded that nuclear fusion occurs in the aeciospores and meiosis in the developing germ tubes, i.e., the number of nuclei was considered as evidence for nuclear fusion and meiosis, although no actual phases of meiotic division in the germ tubes were reported. Functionally such aeciospores would represent teliospores and the germ tubes basidia. The reliability of this report and the justification of the subsequently described endocyclic genus *Endocronartium* Y. Hirats. (e.g., Hiratsuka 1969) have been questioned by various authors (Laundon 1976; Epstein and Buurlage 1988; Vogler and Bruns 1993; Vogler et al. 1997; Kaitera et al. 1999; Hantula et al. 2002).

When Hiratsuka (1968) extended his studies on *Cronartium flaccidum* and *Peridermium pini*, he found that the functionally different aeciospores of the two taxa can be distinguished morphologically by their germ tubes. In contrast, Kaitera et al. (1999) also examined morphological variation of *Peridermium pini* and *C. flaccidum* aeciospores and their germ tubes and found no diagnostic differences. Hantula et al. (2002: 203) wrote "According to previous molecular and morphological analyses, *Cronartium flaccidum* and *Peridermium pini* are very closely related despite differences in their life-cycles. ... Analyses of genetic variation suggested that pine rusts *C. flaccidum* and *P. pini* belong to the same species." According to Hantula et al. (2002), the two rusts do not differ in symptomatology and aeciospore morphology, and can only be separated by inoculation experiments. However, more recent molecular genetic evidence from N Fennoscandia (Samils et al. 2021) showed "that the two life cycle forms are clearly differentiated and occur in separate populations. Within the life cycle forms, geographic differentiation was evident, probably due to restricted gene flow as well as connection with different alternating hosts. The host alternating form dominated in the epidemic regions in northern Fennoscandia."

Cronartium flaccidum and *C. pini* cause serious diseases on two-needle hard pines in Europe. Great losses were reported from N Europe (*C. pini*) and Italy (*C. flaccidum*). The symptomatology is more conspicuous when old trees are affected. After some years the tree top becomes bare. The base of the dry and bare top of otherwise green crowns is characterised by resin flow ('resin top' or 'Kienzopf" disease). Canker (lesion) formation and resin flow on branches or stems kill parts of the crown. If the lower part of the stem is affected, the whole tree dies (e.g., Butin 1989).

For information on nomenclature and taxonomy see Laundon (1976), Hiratsuka (1995), Vogler and Bruns (1993), and Hantula et al. (2002). Whether the pine-to-pine rust *Cronartium pini* occurs in Austria remains uncertain (Poelt and Zwetko 1997: 58–59).

(3) *Cronartium quercus* (Brond.) J. Schröt. ex Arthur

Syn. *Uredo quercus* Brond. [in Duby]; *Cronartium quercuum* s. Gäumann (1959); *C. quercuum* s. Brandenburger (1985); ?*C. asclepiadeum* var. *quercuum* Berk.; ?*C. quercuum* (Berk.) Miyabe ex Shirai

Life cycle insufficiently known:

(II,III? on: *Quercus petraea*, *Qu. pubescens*, *Qu. robur*)

Spermatogonia and aecia wanting. – **Uredinia** hypophyllous, somewhat pustular, 0.25 mm in diam., opening with an apical pore, at length surrounded by the torn epidermis, yellow; peridium delicate or wanting. – **Urediniospores** obovoid to broadly ellipsoid, orange-yellow, 15–25 × 10–17 µm; wall hyaline, 3 µm thick, evenly echinulate with short, strong points. – Telia mostly lacking in European records. – Reference: Wilson and Henderson (1966: 3–4).

Remarks. Infection with *Cronartium quercus* is most frequent on sucker shoots of felled trees. This rust seems to be quite different from the American species on oak, which has larger urediniospores (20–32 × 15–20 µm). Whether it differs from the Japanese rust on oak with only slightly larger spores (24 × 19 µm), is more doubtful (Wilson and Henderson 1966). Both in Japan and in N America (see Arthur 1934), the oak rusts have been shown to have aecial stages on pines on which they form characteristic globoid galls, but these are unknown in Europe. Teliospores have been recorded once in Europe in S France (Viennot-Bourgin 1956). *Cronartium quercus* occurs mainly in S and W Europe, and it seems that the taxonomic affiliations of these records are still unresolved. So far, this rust has not been recorded in Austria.

4 *Cronartium ribicola* J.C. Fisch.

Fig. 18

Hetereuform:

0,I on: *Pinus flexilis*?, *P. strobus*, (*P. aristata*, *P. cembra*, *P. koraiensis*, *P. monticola*, *P. peuce*, *P. wallichiana*)

II,III on: *Ribes alpinum*, *R. aureum*, *R. nigrum*, *R. rubrum*, *R. rubrum* agg., *R. uva-crispa*, *R. uva-crispa* agg., (*R. petraeum*, *R. sanguineum*, *R. spicatum*)

Spermatogonia intracortical, irregular in outline, 2–3 mm in size, 34–67 µm high. – **Aecia** on slightly swollen parts of branches and trunks, erumpent from the cortex, often in large groups clasping around the whole branch or stem; peridium inflated, 2–7 mm long, 2–3 mm wide and 2–2.5 mm high, of 2 or 3 cell layers; outer cell walls c. 5 µm thick, smooth in the upper part of the peridium. – **Aeciospores** oval, subglobose or slightly polyhedral, 22–29 × 18–20 µm; wall hyaline, verrucose but with a nearly smooth area with fused warts; warts bacilliform (annulate in SEM), their central points 1.5–2 µm apart; verrucose wall area 2–2.5 µm thick, smooth area thicker, 3–3.5 µm. – **Uredinia** hypophyllous, evenly dispersed in yellow leaf spots; peridium opening with an apical pore. – **Urediniospores** oval, usually somewhat irregular, 21–25 × 13–18 µm, more rarely elongate, c. 30 × 11 µm; wall hyaline, c. 1.5 µm thick; warts acute, 2–3 µm apart. – **Telia** (teliospore columns) evenly dispersed in large groups, later often over the whole leaf surface, yellowish-brown, 1–1.5 mm long, 60–130 µm thick. – **Teliospores** 35–70 × 11–21 µm. – Reference: Gäumann (1959: 85–86).

Remarks. *Cronartium ribicola* has made the cultivation of *Pinus strobus* and related pine species impossible in Central Europe. Its epidemic spread was depicted in detail by Gäumann (1959). In some years, considerable damage was also observed on the telial hosts, especially on *Ribes nigrum*. Records on *Pinus* are much less common than on *Ribes* (Poelt and Zwetko 1997: 58), but in such cases this might also be due to the lack of herbarium documentation. The aecial hosts observed in the nursery of the Botanical Garden in Graz were young five-needle pines identified as *Pinus* cf. *flexilis* (det. Erwin Gruber) and *P.* cf. *strobus*.

Rossmanomyces Aime & McTaggart (*Chrysomyxa* p.p.)

N.B.: Descriptions of the species now separated under the name *Rossmanomyces* were missing in the original manuscript and have been supplemented in line with the species concept favoured by Peter Zwetko.

This genus has been separated from *Chrysomyxa* rather recently (Aime and McTaggart 2020) and differs in forming a systemic sporothallus [dikaryotic mycelium] in Ericaceae subfam. Pyroloideae (*Pyrola*, *Moneses*, *Orthilia*). The gametothalli [haploid mycelium] are produced on *Picea* and are systemic within the cones, in contrast to gametothalli of *Chrysomyxa* species, which infect needles (Aime and McTaggart 2020). See also Savile (1950, 1955b, under *Chrysomyxa*) for descriptions of species.

1 *Rossmanomyces monesis* (Ziller) Aime & McTaggart

Syn. *Chrysomyxa monesis* Ziller; *Ch. pyrolata* (Körn.) G. Winter s.l.

Heteropsis-form with secondary aecia:

(0,Ia on: *Picea*) – not found in Europe so far (Klenke and Scholler 2015)

Ib,III on: *Moneses uniflora*

Spermatogonia and primary aecia not found in Europe so far. Secondary aecia and telia appear simultaneously in spring, secondary aecia also in summer but without telia. – **Secondary aecia** (uredinia) conical, without a peridium but rupturing like an 'aecidioid aecium', yellow to orange, small, evenly dispersed in large numbers. – **Secondary aeciospores** (urediniospores) 19–33 × 13–24 µm, coarsely verrucose. – **Telia** yellow-red to blood-red, brown when dry, wax-like. – **Teliospores** catenulate, chains 100–400 µm long, single teliospores 12–26 × 6–10 µm. – References: Ziller (1954: 436–437), Klenke and Scholler (2015: 561).

Remarks. In Europe, *Rossmanomyces monesis* has been found only in Austria and Switzerland (e.g., Klenke and Scholler 2015). – For records of *R. monesis* in Austria see Poelt and Zwetko (1997: 49, as *Chrysomyxa m.*).

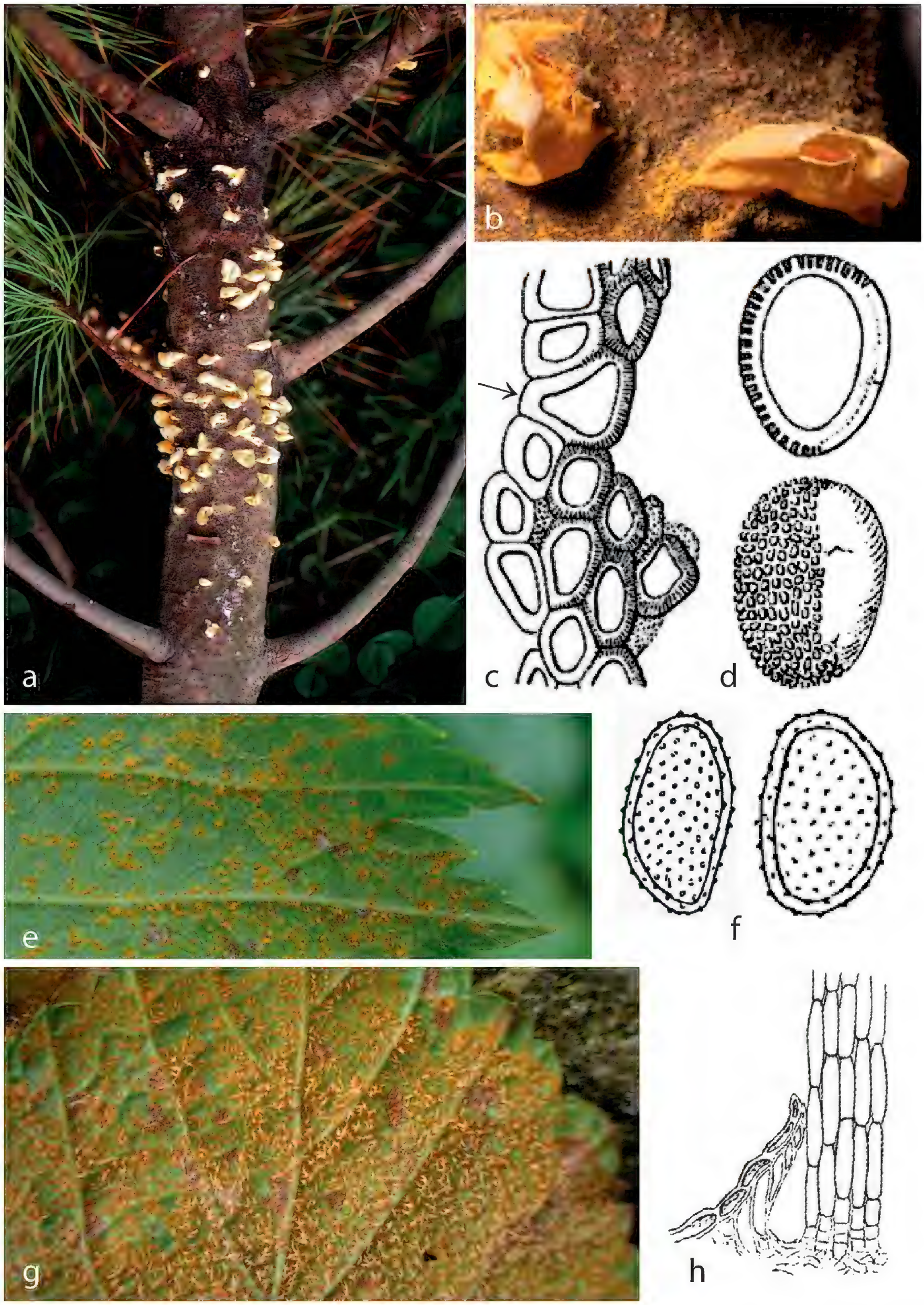


Figure 18. *Cronartium ribicola*. **a–d.** On *Pinus*: **a.** Aecia breaking through the stem bark of a young tree (*Pinus* cf. *flexilis*); **b.** Aecia with irregularly ruptured peridium and orange coloured spore mass; **c.** Peridium cells of an aecium in longitudinal section, note the ± smooth outside (arrow); **d.** Aeciospores; the broad smooth area on one side is also visible in LM, both in optical section and in surface view; **e–h.** On *Ribes nigrum*: **e.** Uredinia; **f.** Urediniospores; **g.** Teliospore columns (telia) on leaf; **h.** Longitudinal section through the base of a telium emerging from an uredinium; note the uredinial peridium under the host epidermis around the base of the telium; (**c, d, f, h** from Klebahn 1914: 722; **e, g** by Julia Kruse).

2 *Rossmanomyces pyrolae* (Rostr.) Aime & McTaggart s.str.

Fig. 19

Syn. *Chrysomyxa pyrolae* Rostr.; *Ch. pyrolata* (Körn.) G. Winter s.str.; *Ch. pirolatum* (Körn.) G. Winter (orthogr. var.)

Heteropsis-form with secondary aecia:
0,Ia on: *Picea abies*, (*P. glauca*, *P. mariana*)
Ib,III on: *Pyrola rotundifolia*, (*Moneses uniflora*, *Pyrola chlorantha*, *P. minor*, *P. media*)

Spermatogonia on the outside (under side) of cone scales, inconspicuous, at first subepidermal, numerous, flat, forming confluent structures 0.6–0.9 mm in size, 50–100 µm high. – **Primary aecia** on the outside (under side) of cone scales, usually forming 1 or 2 inflated, often confluent swellings, up to 5 mm or larger; peridium white but initially covered by a brownish layer of cone scale tissue, later disintegrating. – **Primary aeciospores** formed in chains with intercalary cells, ellipsoidal, 25–36 × 20–30 µm; wall 4–5 µm thick, verrucose; warts prismatic, 3–4 µm thick; contents orange. – **Secondary aecia** (uredinia) hypophyllous, evenly dispersed over large areas or the whole leaf surface. – **Secondary aeciospores** (urediniospores) formed in chains with intercalary cells, ellipsoidal to subglobose or slightly polyhedral, 21–28 × 18–21 µm; wall c. 2 µm thick, hyaline, coarsely verrucose; warts 1.5 µm thick or larger, their central points 2–3 µm apart. – **Telia** small, c. 0.5 mm in diam., circular or elongate, evenly dispersed over large areas or the whole leaf surface, occasionally almost confluent, wax-like, yellowish-red, later dark red, brown when dry. – **Teliospores** catenulate, chains 100–200 µm long, c. 8 µm thick. – **Basidiospores** globose, 7–8 µm in diam. – References: Gäumann (1959: 103), Wilson and Henderson (1966: 61).

Remarks. For scanning electron micrographs of the surface ornamentation of the primary aeciospores of *Rossmanomyces pyrolae* see also Littlefield and Heath (1979), for those of the secondary aeciospores see also Berndt (1999b). Both kinds of aeciospores lack smooth longitudinal strips. Littlefield and Heath (1979) emphasised that a somewhat different annulate wart structure occurs in primary aeciospores of *R. pyrolae*. The warts in *R. pyrolae* consist of only two stacked, cushion-like discs, one on top of the other, while the annulate warts in aeciospores of *Coleosporium* spp. and *Cronartium* spp. appear as irregular stacks of usually five to eight discs in longitudinal section in TEM. Also our scanning electron micrographs show that in primary aeciospores of *R. pyrolae* the two discs are sitting on a high pedestal with inconspicuous, longitudinal ridges. The ridges themselves resemble strings of pearls. We found similar structures in aeciospores of *Cronartium ribicola* and *Melampsorella elatina*. We suppose that the pedestal consists of stacks of discs with a humpbacked margin, while the two uppermost discs have an only slightly pleated margin. Between neighbouring warts, we observed strings or thin arched connections. In some spores, pairs or small groups of warts are not isolated. The possible function of this very complicated surface ornamentation of the primary aeciospores is obscure. Hofsten and Holm (1968) supposed that it will give added buoyancy to the air-borne spore. Sato and Sato (1982) stated that the processes on aeciospores of *Rossmanomyces pyrolae* and *Pucciniastrum fagi* are connected by reticulately arranged narrow ridges. – For records of *R. pyrolae* in Austria see Poelt and Zwetko (1997: 49, as *Chrysomyxa pirolatum*).

For a key to rusts on cone scales of *Picea* see below under *Thekopsora areolata* (p. 207).

3 *Rossmanomyces ramischiae* (Lagerh.) Aime & McTaggart

Syn. *Chrysomyxa ramischiae* Lagerh.; *Ch. pyrolata* (Körn.) G. Winter s.l.

Life cycle insufficiently known (autopsis-form?):
Ia+b,III on: *Orthilia secunda* (*Ramischia s.*)

Spermatogonia absent; morphological characters of other sori and spores as in *Rossmanomyces pyrolae*. – **Primary aecia** (primary uredinia) small, densely and evenly dispersed, appearing simultaneously with the telia in spring. – **Secondary aecia** (secondary uredinia) larger, loosely dispersed, appearing on the same leaves in summer, but without telia. – Reference: Gäumann (1959: 105).

Remarks. The life cycle of *Rossmanomyces ramischiae* is not fully clarified yet. According to Gäumann (1959), it could be a brachy-form with primary and secondary uredinia. However, the spores in these sori are formed in chains with intercalary cells. Therefore, the sori are aecia and the life cycle should be an autopsis-form. – For a record of *R. ramischiae* in Austria see Poelt and Zwetko (1997: 49, as *Chrysomyxa r.*).

Thekopsora Magnus (*Pucciniastrum* p.p.)

Prior works consider *Thekopsora* and *Pucciniastrum* as congeneric or confamilial (fam. Pucciniastraceae). Currently the genus *Thekopsora* s.str., as typified by *Th. areolata*, pertains to Coleosporiaceae (Aime et al. 2018a: 148, fig. 3; Aime and McTaggart 2020: 33, fig. 2).

The following brief diagnosis is mainly based on the type species, *Thekopsora areolata* (e.g., Gäumann 1959: 53–57; Brandenburger 1985: 1036). – Spermatogonia and aecia on *Picea*, uredinia and telia on various families (here only Rosaceae and Ericaceae). Spermatogonia subcuticular. Aecia peridermioid, subepidermal, later erumpent. Uredinia subepidermal, with flat-hemispherical to conical peridium and ± differentiated, smooth or ornamented ostiolar cells. Telia forming ± effuse crusts, at first red or purple, later brown. Teliospores (mostly?) dormant, intraepidermal, with anticlinal septa, 2- to 6-celled (usually 4-celled); wall ± pigmented; germ pores inconspicuous.

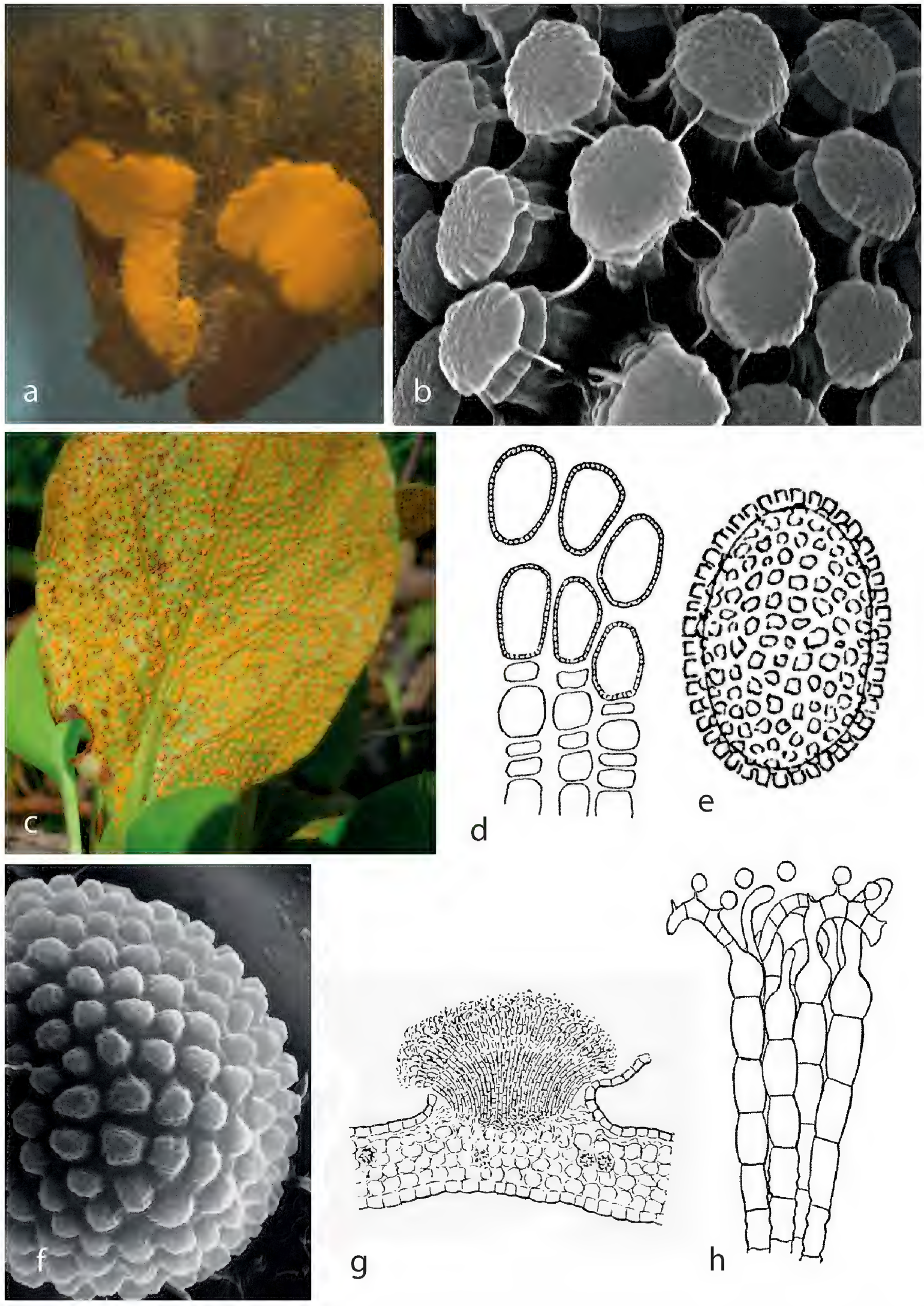


Figure 19. *Rossmanomyces pyrolae*. **a, b.** On *Picea abies*: **a.** Primary aecia on abaxial side of a cone scale; **b.** Annulate wall ornaments of a primary aeciospore in SEM; in contrast to the annulate ornaments of related Melampsorineae, these consist of only two disc-like elements on a stout foot; **c–h.** On *Pyrola minor*: **c.** Secondary aecia (uredinia); **d.** Chains of secondary aeciospores (urediniospores); **e.** Secondary aeciospore; **f.** Wall of secondary aeciospore with dome-shaped ornaments in SEM; **g.** Telium in median section; **h.** Germinating teliospores with basidia and basidiospores; (**a** by Waldschutz Schweiz WSL, with permission; **b, f** from Zwetko and Blanz 2018: 281; **c** by Julia Kruse; **d, e, g, h** from Klebahn 1914: 722).

1 *Thekopsora agrimoniae* Dietel

Fig. 20

Syn. *Pucciniastrum agrimoniae* (Dietel) Tranzschel; *Uredo potentillarum* DC. var. *agrimoniae-eupatoriae* DC.; *Pucciniastrum agrimoniae-eupatoriae* (DC.) Lagerh.; *Quasipucciniastrum ochraceum* (Bonord.) M. Scholler & U. Braun

Probably hemi-form, but life cycle insufficiently known:
II,III on: *Agrimonia eupatoria*, (*A. procera*)

Spermatogonia and aecia unknown. – **Uredinia** mainly hypophyllous, in groups or ± covering the whole surface, long covered by the epidermis, pustular, with a hemispherical peridium, 0.1–0.5 mm in diam., opening with a pore; ostiolar cells thick-walled (2.5–5 µm) and echinulate at opening; wall of other peridial cells 1.5–2 µm thick, smooth; spore mass (yellow-)orange. – **Urediniospores** 15–25 × 12–20 µm; wall hyaline, 1–1.5 µm thick, finely echinulate; germ pores indistinct. – **Telia** hypophyllous, in proximity to uredinia, subepidermal, forming small, inconspicuous, reddish-brown crusts. – **Teliospores** intercellular, formed underneath the epidermis, mainly divided into 4 cells by two anticlinal septa, sometimes 2-, 3- or 5-celled, 15–25 µm in diam., 20–25 µm high (in vertical section); wall 2 µm thick, not thickened at the apex, yellowish-brown, smooth; germ pores obscure. – References: Gäumann (1959: 48), Helfer (2005: 356).

Figure 20. *Thekopsora agrimoniae* on *Agrimonia eupatoria*: uredinia (photo by Julia Kruse).

Remarks. Probably *Thekopsora agrimoniae* can maintain itself by overwintered urediniospores (Gäumann 1959). Scholler et al. (2022) place this species in the genus *Quasipucciniastrum* X.H. Qi, P. Zhao & L. Cai, but we prefer to follow Aime and McTaggart (2020: 33, fig. 2). – For records of *Th. agrimoniae* in Austria see Poelt and Zwetko (1997: 248, as *Pucciniastrum a.*).

2 *Thekopsora areolata* (Fr.) Magnus

Fig. 21

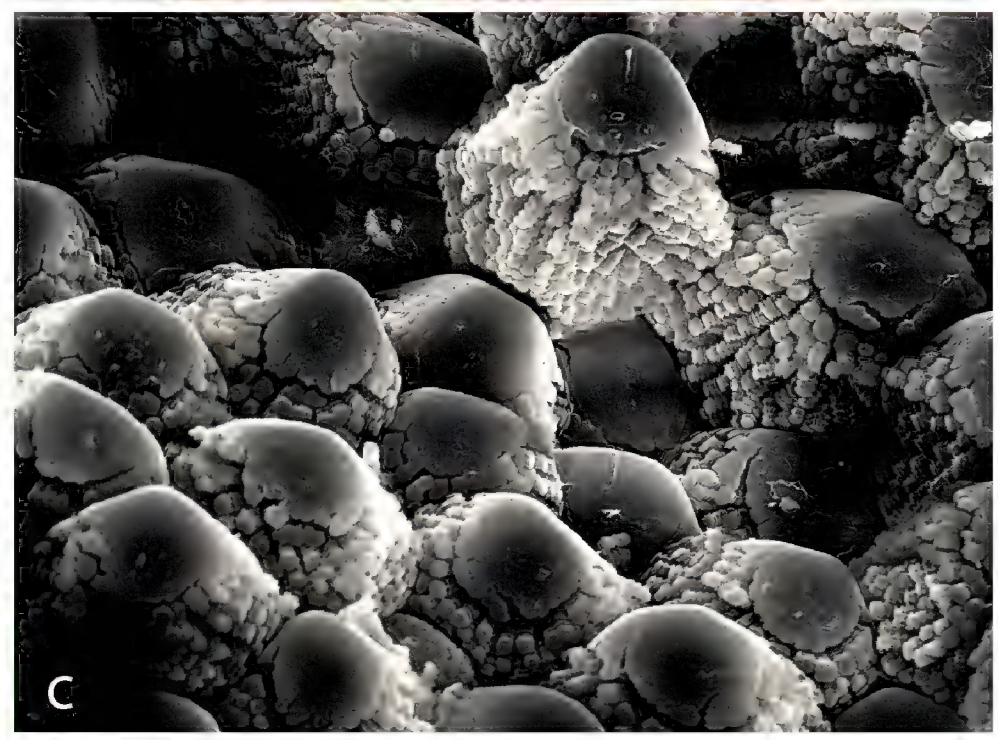
Syn. *Pucciniastrum areolatum* (Fr.) G.H. Otth

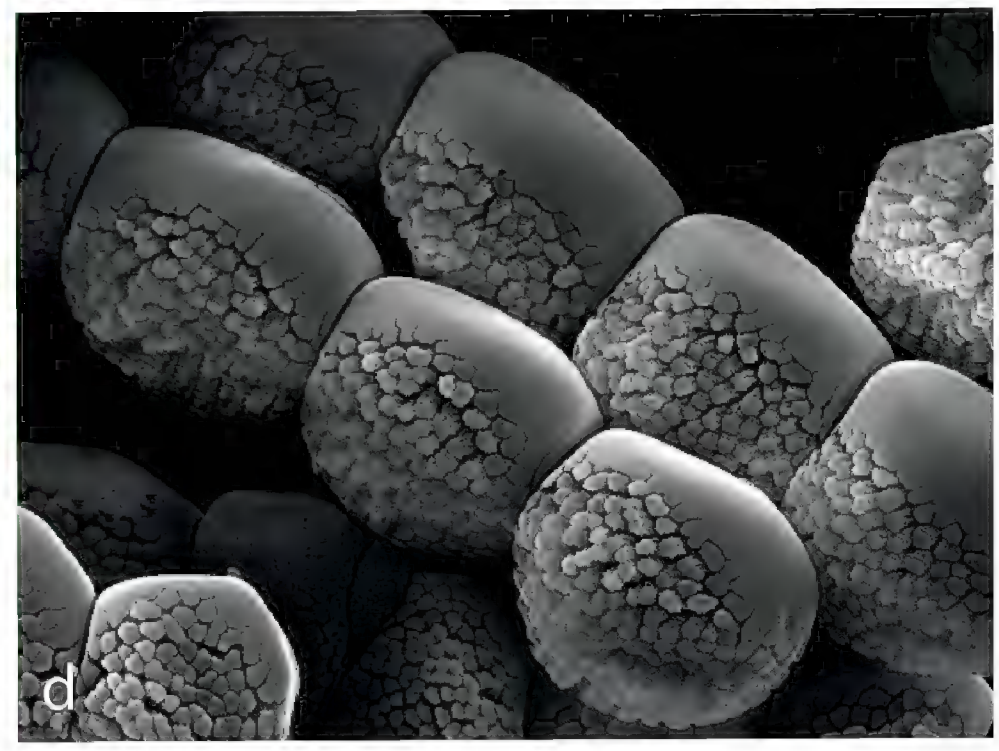
Hetereu-form:
0,I on: *Picea abies*
II,III on: *Prunus padus*, *P. virginiana*
(II,[III] on: *Prunus avium*, *P. cerasus*, *P. domestica*, *P. insititia*, *P. mahaleb*, *P. padus* subsp. *borealis*, *P. serotina*, *P. spinosa*)

Spermatogonia subcuticular, abaxial on cone scales, joining and forming irregular flat crusts up to 4 mm in diam., in inoculation experiments also on young shoots of the tree-top, whitish, exuding a sugary liquid with strong smell. – **Aecia** mainly on the inner side of the cone scales, sometimes on the outer side, on all scales of the cone, crowded, subepidermal, erumpent, yellowish-brown(-orange) to (reddish-)brown, 1–1.25 mm in diam., 0.7–1 mm high. Peridium hemispherical or angular by mutual pressure, firm, hard, brown, rupturing and becoming cupulate when mature; peridial cells irregularly polygonal, 22–30 × 22–25 µm; outer wall extremely thick (17–22 µm), almost completely displacing cell contents, slightly verrucose; inner wall thinner (2.5–3.5 µm), finely verrucose; spore mass yellow-grey. – **Aeciospores** globoid to angular, 20–28 × 16–22 µm, in regular chains; wall hyaline, laterally with a narrow, smooth strip (where the thickness is only 3 µm), for the most part 3–6 µm thick, densely and pronouncedly verrucose, with anticlinal striations in optical section; warts column-shaped (annulate in SEM); germ pores obscure. – **Uredinia** hypophyllous, in groups, in purplish to reddish-brown leaf spots (1–5 mm in diam.) bordered by the fine leaf veins, long covered by the epidermis, pustular, with a hemispherical peridium, opening with a pore; ostiolar cells very thick-walled, smooth; spore mass whitish to yellowish even when fresh (some authors, however, describe the colour of the uredinia as 'orange-yellow'). – **Urediniospores** 15–21(–24) × 10–15 µm, obovoid to ellipsoid; wall hyaline, 1.5–2 µm thick, finely echinulate; spine distance ca. 2 µm; germ pores obscure; contents orange-yellow when fresh; pedicels short. – **Telia** mainly epiphyllous, occasionally hypophyllous, forming dark reddish-brown or blackish-brown crusts delimited by leaf veins, sometimes 10 mm long, sometimes rather small, glossy in appearance. Within these crusts nearly all epidermis cells are filled with teliospores. – **Teliospores** dormant, formed within the epidermis cells, mainly divided into (2–)4(–5) cells by anticlinal septa, 22–30 µm long, 8–14 µm wide; wall 1 µm thick at base, 2–3 µm at apex, light brown, smooth; 1 germ pore in each cell in the corner where the anticlinal walls meet. – Description after Gäumann (1959: 53–57) and Helfer (2005: 357), modified.

Remarks. Usually the aecia of *Thekopsora areolata* are produced on cones, but sometimes also on young stems of *Picea* where the rust can cause twisting and distortion. The infection of the young cones happens at the time of pollination in spring. Spermatogonia are produced soon after. Aecia begin to grow in summer on the early tanned scales of the cones; they ripen next spring (Gäumann 1959). – For the distribution of *Th. areolata* in Austria see Poelt and Zwetko (1997: 252, as *Pucciniastrum areolatum*).

A key for all rust genera and species with uredinia and telia on *Prunus* is attached to *Leucotelium cerasi* (p. 312).





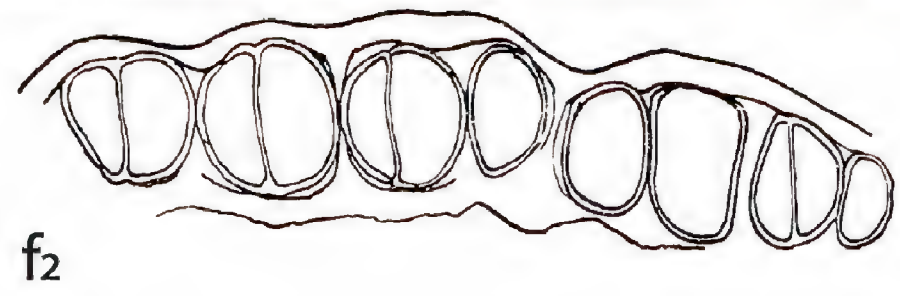


Figure 21. *Thekopsora areolata*. **a–d.** On *Picea abies*: **a.** Cone with aecia on adaxial side of the cone scales; **b.** Single cone scale with aecia; **c, d.** Aeciospores in SEM: **c.** view into an aecium after manually opening the peridium, showing the apical smooth caps of the spores; **d.** Chains of aeciospores; every aeciospore with a longitudinal smooth overlay connecting apex and base on one side; **e–f.** On *Prunus padus*: **e.** Light-brown hypophyllous uredinia in a small purplish leaf spot; **f1, f2.** Intraepidermal teliospores in surface view and vertical section; (**a** from Dietel 1928: 39, with permission from Duncker & Humblot GmbH; **c, d** from Zwetko and Blanz 2018: 276; **f** from Fischer 1904: 464, as *Pucciniastrum padi*, with permission from Bryolich).

Key to the rusts on cone scales of *Picea*

(these two rusts differ also in surface ornamentation of aeciospores – see diagnoses)

1a Aecia often on the inner side of the cone scales, densely crowded, hemispherical, 1–1.25 mm in diam., (reddish-) brown. Spore mass yellow-grey. Peridia firm, hard, brown, rupturing and becoming cupulate when mature, honeycomb-shaped through crowding ..... *Thekopsora areolata*

1b Aecia often on the outer side of the cone scales, one to few on each scale, forming swellings, roundish or oblong in shape, very large, 5 mm or even more in diam. Spore mass orange. Peridia at first convex, white, usually covered by reddish-brown tissue of the cone scale, later evanescent and spore mass becoming pulverulent ..... *Rossmanomyces pyrolae* (p. 203)

(3) *Thekopsora ericae* (A. Naumann) Tranzschel

Syn. *Uredo ericae* A. Naumann; *Pucciniastrum ericae* (A. Naumann) Cummins; *Thekopsora fischeri* Cruchet

Life cycle insufficiently known:

(II on: *Calluna vulgaris*, *Erica gracilis* cult., *E. hiemalis* cult.)

Spermatogonia, aecia and telia unknown. – **Uredinia** hypophyllous, small, up to 0.13(–0.2) mm in diam., usually arising below a stoma, pustular, yellow; peridium opening with a pore. – **Urediniospores** 19–25 × 13–17 µm, irregularly ovoid or globoid; wall about 1 µm thick, hyaline, finely echinulate; distance of spines about 1.5–2 µm; contents orange when fresh. – Reference: Gäumann (1959: 63).

Remarks. The uredinia-producing mycelium of *Thekopsora ericae* causes 'witches' brooms', and affected plants are conspicuous in the field, but the distortions caused by *Th. ericae* are less extreme than those by *Calyptospora columnaris* (*C. goeppertiana*). Damage on cultivated *Erica* species is reported from Switzerland. So far, this rust has not been recorded in Austria.

4 *Thekopsora pyrolae* (H. Mart.) P. Karst.

Syn. *Pucciniastrum pyrolae* (H. Mart.) J. Schröt.; *P. pyrolae* (J.F. Gmel.) Dietel

Probably hemi-form:

II,III on: *Moneses uniflora*, *Orthilia secunda*, *Pyrola chlorantha*, *P. minor*, *P. rotundifolia*, (*Chimaphila umbellata*, *Pyrola media*)

Spermatogonia and aecia unknown. – **Uredinia** mostly hypophyllous, sometimes on petioles, in small groups, causing reddish, reddish-brown or yellowish spots on the upper surface of the leaf, long covered by the epidermis, pustular, with a firm, hemispherical peridium, 0.1–0.4 mm in diam., opening with a pore, ± orange-yellow or brownish-yellow; wall of ostiolar cells greatly thickened below, coarsely to sparsely aculeate above; spore mass orange-yellow. – **Urediniospores** 28–32 × 14–16 µm; wall hyaline, 1.5–2.5 µm thick, finely echinulate; contents orange-yellow when fresh; germ pores obscure. – **Telia** hypophyllous, subepidermal, inconspicuous, forming an even layer of laterally united cells. – **Teliospores** 24–28 µm long, 10–12 µm wide; wall uniformly thin, about 1 µm, hyaline. – References: Gäumann (1959: 50), Wilson and Henderson 1966: 37–38.

Remarks. The mycelium of *Thekopsora pyrolae* overwinters in the evergreen leaves of its hosts (Gäumann 1959). Another rust species with yellow-orange sori occurs on *Moneses* and *Pyrola*, *Rossmanomyces pyrolae* (syn. *Chrysomyxa pyrolata*). The secondary aecia (uredinia) of this rust often cover the whole surface of the leaf uniformly and densely (Fig. 19c, p. 204). They have very delicate evanescent peridia and spores with coarse warts. Hence it does not cause difficulties to distinguish these two rusts. – For records of *Th. pyrolae* in Austria see Poelt and Zwetko (1997: 250, as *Pucciniastrum p.*).

5 *Thekopsora sparsa* (G. Winter) Magnus

Fig. 22

Syn. *Pucciniastrum sparsum* (G. Winter) E. Fisch.

Hetereu-form:

0,I on: *Picea abies*

II,III on: *Arctostaphylos alpinus*, *A. uva-ursi*

Spermatogonia subcuticular, 70–100 µm in diam., 35 µm high. – **Aecia** on needles of current season, not causing conspicuous leaf spots, erumpent, cylindrical, with a firm peridium, up to 0.5 mm high, pale reddish; spore mass yellowish-orange. – **Aeciospores** globoid or ellipsoid, 21–32 × 18–25 µm; wall hyaline, 1 µm thick, with

Figure 22. *Thekopsora sparsa* on *Arctostaphylos alpinus*: uredinia (photo by Julia Kruse).

a small smooth sector, but densely and coarsely verrucose for the most part. – **Uredinia** hypophyllous, small, in small leaf spots which are carmine-red on the upper surface of the leaf, pustular, with a hemispherical peridium, opening with a pore, yellow or yellowish-orange; ostiolar cells thick-walled, with cone-shaped projections towards the pore, finely echinulate on the outside. – **Urediniospores** 28–42 × 14–18 µm, ellipsoid to clavoid; wall hyaline, 1.5 µm thick, echinulate. – **Telia** epiphyllous, in leaf spots. – **Teliospores** formed within the epidermis cells, divided into 4–8 cells by anticlinal septa, 18–35 µm in diam., 24–35 µm high (in vertical section); wall 1.5–2 µm thick, thickened at the apex (up to 6 µm), brown, with 1 germ pore in each cell in the corner where the anticlinal walls meet. – Reference: Gäumann (1959: 61).

Remarks. Aecia on leaves of *Picea abies* can be distinguished in the field: *Chrysomyxa* species cause conspicuous leaf spots, *Thekopsora sparsa* does not. – For records of *Th. sparsa* in Austria see Poelt and Zwetko (1997: 253–254).

Melampsoraceae Kleb. s.str.

The Melampsoraceae s.str. proved to be clearly monophyletic and separate from the other families of the Melampsorineae by a long genetic distance (e.g., Maier et al. 2003; Pei et al. 2005a; Aime 2006). In Central Europe, it is only represented by its type genus *Melampsora*.

The distinguished position of the Melampsoraceae s.str. within the Melampsorineae is not only emphasised by morphological characters (e.g., caeomoid aecia) and molecular genetic data, but also by the host range. All genera of the Melampsorineae grow on conifers in their aecial state, but only *Melampsora* has been able to expand the host range of the aecial state to mono- and dicotyledonous angiosperms. This indicates an evolution of this genus separate from the other genera for a long time.

In addition to host range and molecular genetic characters, there are also major differences in both aecia and uredinia morphology when comparing Melampsoraceae s.str. to the other families in suborder Melampsorineae. Aecia of *Melampsora* have no peridia or only few peridial cells adherent to the epidermis of the host plant, and its uredinia have no peridia but numerous paraphyses. Wall ornaments of aeciospores and urediniospores of *Melampsora* species under SEM also differ considerably from those of Coleosporiaceae, Milesinaceae and Pucciniastraceae.

The warts on the aeciospore surface of *Melampsora* species are evenly distributed (e.g., Fig. 23), there is no smooth longitudinal strip from apex to base like in other Melampsorineae (e.g., Zwetko and Blanz 2018). Zwetko and Blanz (2018) also figured a remarkable 'gradation' among conifer rusts when they studied the warts proper under SEM: In *Chrysomyxa rhododendri* (and many other Melampsorineae) the 'annulate' ornaments (warts) of primary aeciospores consist of several stacked disks (Fig. 8d, p. 186), in *Rossmanomyces pyrolae* these ornaments are built of two cushion-like discs on a stout base (Fig. 19b, p. 204; see also Littlefield and Heath 1979), and in aeciospores of *Melampsora laricis-epitea* they consist of only two elements, a stout, cylindrical or slightly conical base with a globose structure on top (Fig. 23). Moreover, the bases of neighbouring ornaments are connected by narrow ridges which can also be found in other Melampsorineae, e.g., *Rossmanomyces pyrolae* and *Pucciniastrum fagi* (Sato and Sato 1982).

Anamorphic taxa pertaining to *Melampsora* (or to Melampsoraceae s.str., resp.) have traditionally been placed in the form genera ***Caeoma*** (if only aecia were known) and ***Uredo*** (only uredinia). In accordance with the present ICN (2012, 2018), recent nomenclatural recommendations by Aime et al. (2018b) strongly suggest to interpret *Caeoma* Link as a synonym of *Aecidium* Pers. ex J.F. Gmel. (= *Puccinia* Pers.), and *Uredo* Pers. as a synonym of *Uromyces* (Link) Unger. However, as already

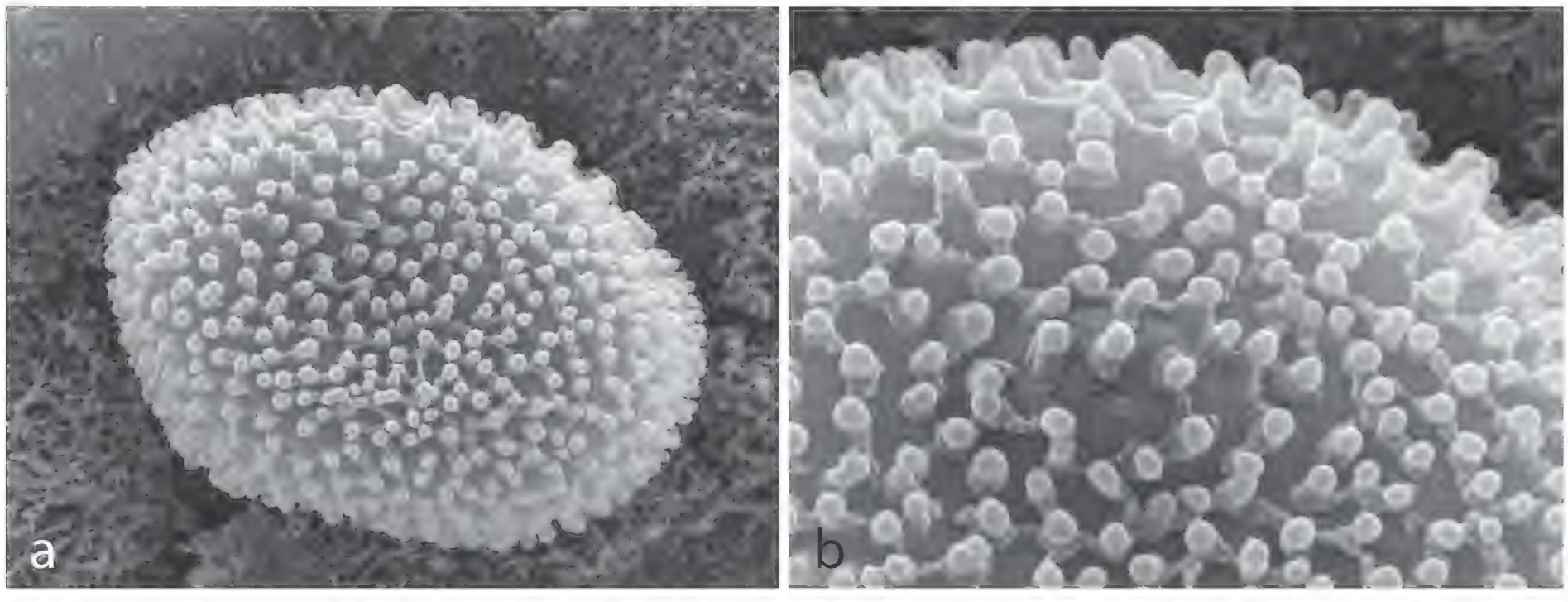


Figure 23. *Melampsora laricis-epitea* on *Larix decidua*, as an example for aeciospore wall ornaments in the Melampsoraceae s.str.: **a.** Spore wall with evenly dispersed ornaments (warts); **b.** The same at higher magnification, showing warts consisting of a stout conical base carrying a depressed-globose element on top. The aeciospore wall lacks the ± smooth longitudinal strip (overlay) found in other Melampsorineae (compare Figs 8c, 16f, 21d on pages 186, 198, 206); (**a, b** from Zwetko and Blanz 2018: 282).

mentioned in the introductory chapter on nomenclature, it will take time to clarify the countless taxa described in form genera like *Caeoma*, *Aecidium* or *Uredo*. In the present work, anamorphic Melampsoraceae s.str. are treated under '*Melampsora* sp.' (see pp. 245–248 below).

In contrast to Laundon (1965a) and Aime et al. (2018b), Cummins and Hiratsuka (2003) regarded *Caeoma saxifragarum* (DC.) Link as the type species of *Caeoma*, a taxon assigned to *Melampsora* and supposedly the aecial stage of *Melampsora vernalis*. However, the genus *Caeoma* in the traditional sense was characterised by the lack of a conspicuous peridium. Taxa described in this genus turn up in rather diverging rust genera (e.g., *Melampsora*, *Phragmidium*, *Chrysomyxa*) and differ, for instance, in the surface morphology of their spores and in the presence or absence of paraphyses.

Melampsora Castagne

Syn. *Caeoma* auct.

Melampsora is a rather large genus of heteroecious and autoecious species. The heteroecious species produce aecia on various families of plants (in our area on Pinaceae, Grossulariaceae, Saxifragaceae, Papaveraceae, Fumariaceae, Celastraceae, Violaceae, Euphorbiaceae, Araceae, Alliaceae, Amaryllidaceae, Orchidaceae). The uredinia and telia of all heteroecious species occur on Salicaceae (*Populus* and *Salix*). Species with aecia on needles of conifers are often regarded as primitive. In Central Europe some species are not obligatorily heteroecious and persist as hemi-forms. The autoecious species (auteu- and autopsis-forms) occur on various dicotyledonous genera (in our area on *Euphorbia*, *Hypericum*, *Linum*, *Saxifraga* and one species on *Salix*). – **Spermatogonia** subcuticular (type 3 of Hiratsuka and Cummins 1963) or subepidermal (type 2), conical or hemispherical. – **Aecia** caeomoid (without peridium or paraphyses but some species have peridial cells adherent to the epidermis of the host plant), subepidermal in origin, erumpent. – **Aeciospores** catenulate, globoid, angular-globoid, or ellipsoid; bright yellow or orange when fresh; wall hyaline, verrucose; the structure of the aeciospore wall is not uniform within the genus. – **Uredinia** subepidermal in origin, erumpent, with abundant clavate or capitate paraphyses; peridium thin, soon evanescent. – **Urediniospores** borne singly on pedicels, globoid or ellipsoid, bright yellow or orange when fresh; wall hyaline, echinulate (some species have a smooth apex); germ pores indistinct. – Kaneko and Hiratsuka (1982) examined the arrangement and number of germ pores in several species. They described the arrangement as scattered or bizonate and counted 4–9 pores. – **Telia** subepidermal or rarely subcuticular, not erumpent, forming crusts consisting of a single layer of spores, orange or brownish when young, dark brown or blackish when mature. – **Teliospores** sessile, 1-celled, adhering laterally, with 1 indistinct apical germ pore; wall usually thin, smooth, brown or brownish.

Rust caused by *Melampsora* spp. is the most damaging disease of willows and hybrid poplars in renewable energy plantations. The identification of these rusts raises difficulties. For keys to the rusts on willows and poplars see under *Melampsora epitea* s.l. (p. 214) and *M. populnea* s.l. (p. 238). The use of binomials like *Melampsora populina* s. latiss. (referring to all *Melampsora* taxa on *Populus*) and *M. salicina* s. latiss. (all taxa on *Salix*) is certainly not recommendable, except if a provisional name for an insufficiently known collection or taxon is required. Especially the delimitation of the accepted taxa within the following groups (species complexes) is still debated and needs further investigation:

***M. epitea* s.l.** (nos 5–14, p. 212–226), on *Salix*: *M. abietis-caprearum*, *M. arctica*, *M. euonymi-caprearum*, *M. lapponum*, *M. laricis-epitea*, *M. repentis*, *M. reticulatae*, *M. ribis-epitea*, *M. ribis-purpureae*.

***M. euphorbiae* s.l.** (nos 15–20, p. 226–231), on *Euphorbia*: *M. euphorbiae* (s. Gäumann 1959), *M. euphorbiae-dulcis*, *M. euphorbiae-gerardianae*, *M. euphorbiae-helioscopiae*, *M. gelmii*.

***M. populnea* s.l.** (nos 28–33, p. 237–243), on *Populus*: *M. laricis-tremulae*, *M. magnusiana*, *M. pinitorqua*, *M. pulcherrima*, *M. rostrupii*.

List of keys to *Melampsora* species:

Key to the *Melampsora* species on *Salix* (p. 214)
Key to rusts on *Euphorbia* (p. 228)
Key to the *Melampsora* species on *Salix caprea* when only uredinia are present (p. 233)
Key to the *Melampsora* species on *Populus* (p. 238)
Key to the *Melampsora* species on *Salix viminalis* (p. 243)
Key to the *Melampsora* species on *Salix retusa* (p. 245)
Key to the rusts on needles of *Abies* (p. 250)

1 *Melampsora allii-fragilis* Kleb.

Figs 24, 25

Hetereu-form:

0,I on: *Allium ursinum*, (*A. ascalonicum*, *A. carinatum*, *A. cepa*, *A. fistulosum*, *A. ochroleucum*, *A. oleraceum*, *A. pulchellum*, *A. sativum*, *A. schoenoprasum*, *A. scorodoprasum*?, *A. lusitanicum* [syn. *A. senescens* subsp. *montanum*], *A. sphaerocephalum*, *A. victorialis*, *A. vineale*)

II,(III) on: *Salix fragilis*, (*S. pentandra*, *S.* ×*rubens*)

Spermatogonia subepidermal, faintly coloured, approx. 200 µm in diam. – **Aecia** amphigenous on leaves, on stems and bulbils, up to 2 mm long and 0.5–l mm wide. – **Aeciospores** irregularly ellipsoid or rarely globoid but usually angular, 18–25 × 12–19 µm; wall 1–2 µm thick, densely verrucose (approx. 4 warts/µm²), warts low and flat. – **Uredinia** hypophyllous, occasionally epiphyllous, small (0.5 mm in diam.), surrounded by ruptured epidermis, orange, causing red spots on the upper side of the leaf.

Figure 24. *Melampsora* cf. *allii-fragilis* on *Allium ursinum*: spermatogonia (arrows) surrounded by a ring of partly confluent aecia.

Paraphyses mainly capitate, 50–70 µm long, apex 15–20 µm in diam., occasionally clavate and 10–15 µm in diam.; wall thickness even, 3–5 µm. – **Urediniospores** distinctly elongated, often thickened at apex, pear-shaped, 22–33 × 13–15 µm; wall thickness 3 µm, with narrow thinner areas (germ pores?), moderately distantly echinulate (0.35 spines/µm²); spores with smooth apex. – **Telia** mainly epiphyllous, occasionally hypophyllous, subcuticular, single or in groups, forming low cushions, 0.25–1.5 mm in size, dark brown, shining. – **Teliospores** prismatic, rounded at both ends, longer in telia on the upper side of the leaf (30–48 × 7–14 µm), smaller and broader on the lower side (20–36 × 12–16 µm); wall thickness even, 1 µm. – References: Gäumann (1959: 157), Helfer (1992: 127).

Remarks. According to Gäumann (1959) and Helfer (1992), *Melampsora allii-fragilis* is almost indistinguishable from *M. galanthi-fragilis* Kleb. apart from its alternate host range. It is closely related to *M. vitellinae* and to *M. allii-populina* (a poplar rust). Aeciospores of *M. allii-fragilis* and *M. vitellinae* are morphologically indistinguishable; those of *M. allii-populina* differ slightly in wall thickness. – For records of *M. allii-fragilis* in Austria see Poelt and Zwetko (1997: 75).

2 *Melampsora allii-populina* Kleb.

Fig. 26

Hetereu-form:

0,I on: *Allium ursinum*, *Arum cylindraceum*, *A. maculatum*?, *Muscari neglectum*?, (*Allium ascalonicum*, *A. carinatum*, *A. cepa*, *A. oleraceum*, *A. sativum*, *A. schoenoprasum*, *A. scorodoprasum*, *A. sphaerocephalum*, *A. suaveolens*, *A. vineale*, *Muscari comosum*)

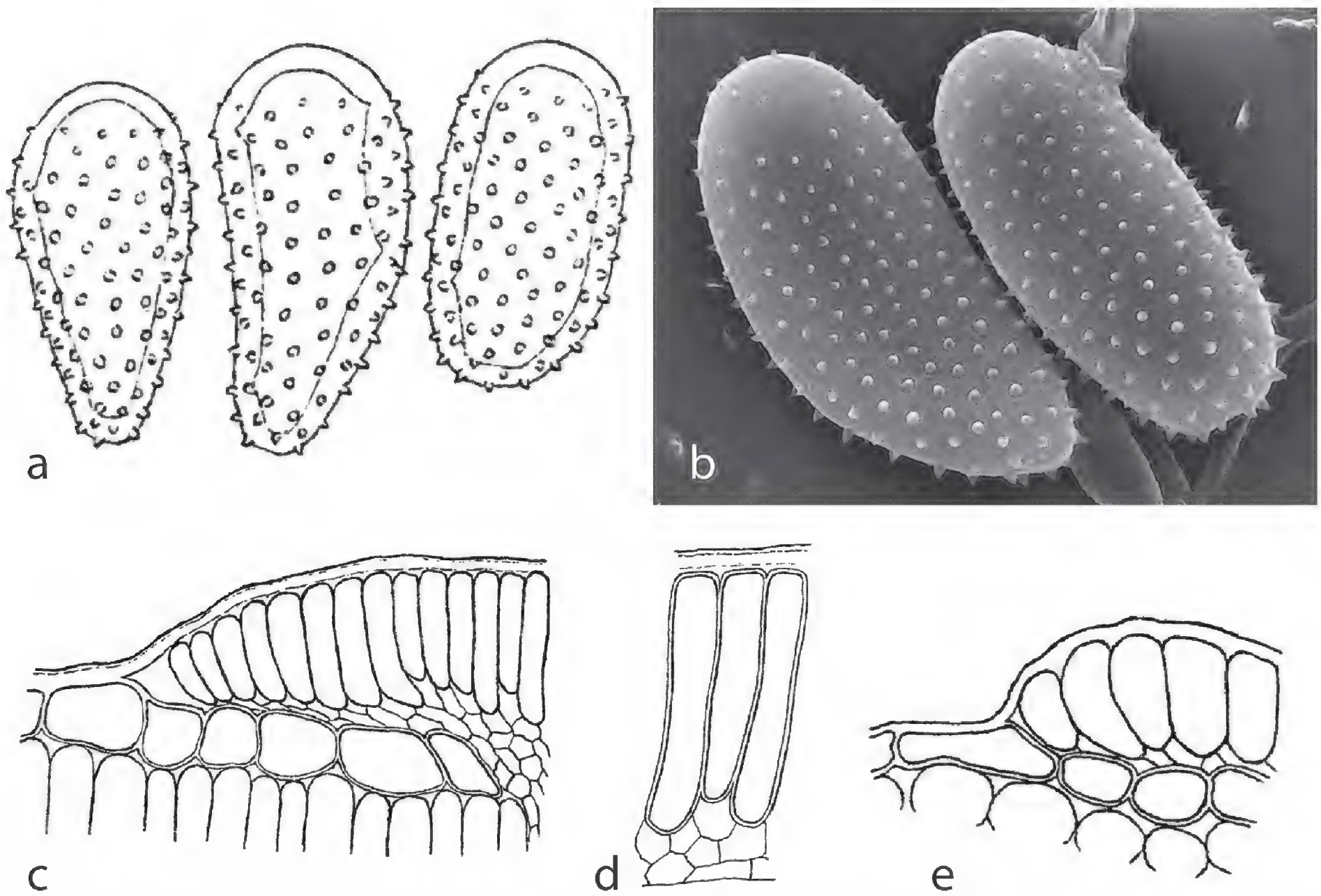


Figure 25. *Melampsora allii-fragilis* on *Salix fragilis*: **a, b.** Urediniospores with (almost) smooth apex; spines increasing in size and density towards the base; spore wall sometimes thinner at certain spots; **c, d.** Telium on the upper side of the leaf in vertical section, teliospores arranged in subcuticular crusts, spore wall evenly thick; **e.** Telium on the lower side of the leaf showing shorter spores; (**a, c, d, e** from Klebahn 1914: 782; **b** by Paul Blanz).

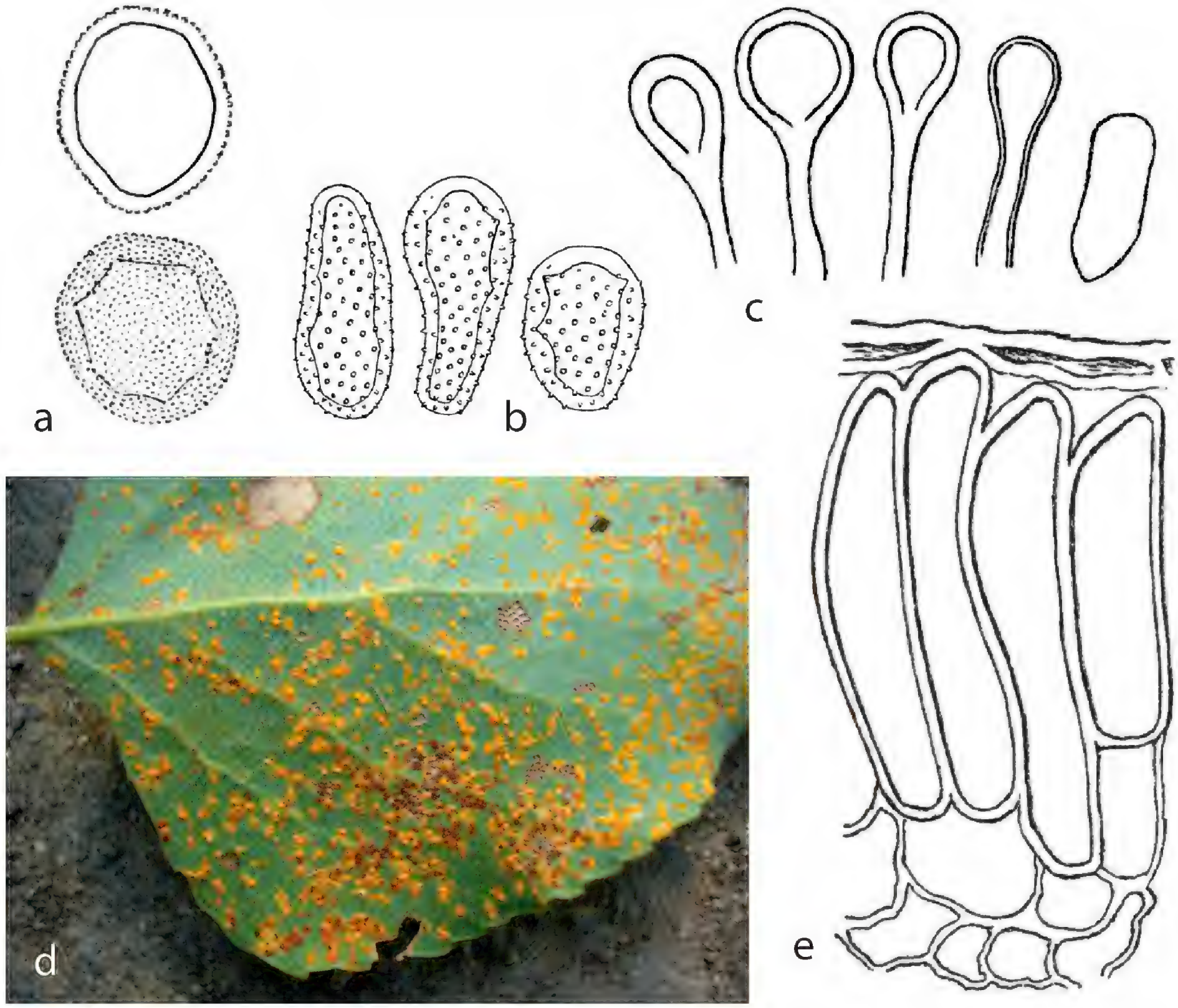


Figure 26. *Melampsora allii-populina*: **a.** On *Allium ascalonicum*: aeciospores, spore wall sometimes thinner at certain spots; **b–d.** On *Populus nigra*: **b.** Urediniospores echinulate but apically smooth, wall thinner at some spots but without equatorial thickening as in *M. laricis-populina*; **c.** Paraphyses with evenly thick walls, size of an urediniospore in comparison; **d.** Hypophyllous uredinia and telia on *Populus* ×*canadensis*; **e.** Teliospores arranged in subepidermal crust, spore walls evenly thick; (**a, b, c, e** from Klebahn 1914: 766; **d** by Julia Kruse).

II,III on: *Populus nigra*, (*P. balsamifera*, *P.* ×*canadensis*, *P. deltoides*?, *P. nigra* cv. *italica*, *P. simonii*)

Spermatogonia yellowish, approx. 100 µm high and 140 µm wide. – **Aecia** about 1 mm in diam., bright orange-red, on yellowish leaf spots, surrounded by the epidermis and a rudimentary peridium. – **Aeciospores** globoid, ovoid or angular-globoid, 17–23 × 14–19 µm; wall about 2 µm thick, but sometimes thicker and then with thin areas, densely verrucose, distance of warts about 1 µm. – **Uredinia** hypophyllous, occasionally epiphyllous, round, small (scarcely 1 mm wide), bright red-orange, producing yellowish leaf spots. Paraphyses mainly capitate, 50–60 µm long, apex 14–22 µm in diam., with thin stalk, occasionally clavate; wall thickness even, 2–3 µm. – **Urediniospores** distinctly elongated, often clavoid or pear-shaped, rarely ovoid, 24–38 × 11–18 µm; wall thickness 2–4 µm, with narrow thinner areas (germ pores?) but without equatorial thickening, distantly echinulate but smooth at the apex; distance of spines 2–3 µm. – **Telia** mainly hypophyllous, subepidermal, single and in groups, scattered over the leaf, 0.25–1 mm in size, blackish-brown, not shining. – **Teliospores** irregularly prismatic, rounded at both ends, 35–60 × 6–10 µm; wall light brown, 1–1.5 µm thick, scarcely thickened above (2 µm). – References: Gäumann (1959: 137–138), Wilson and Henderson (1966: 71–72).

Remarks. For records of *Melampsora allii-populina* in Austria see Poelt and Zwetko (1997: 75).

3 *Melampsora amygdalinae* Kleb.

Fig. 27

Auteu-form:

0–III on: *Salix triandra*, (*S. pentandra*, *S. triandra* × *viminalis*)

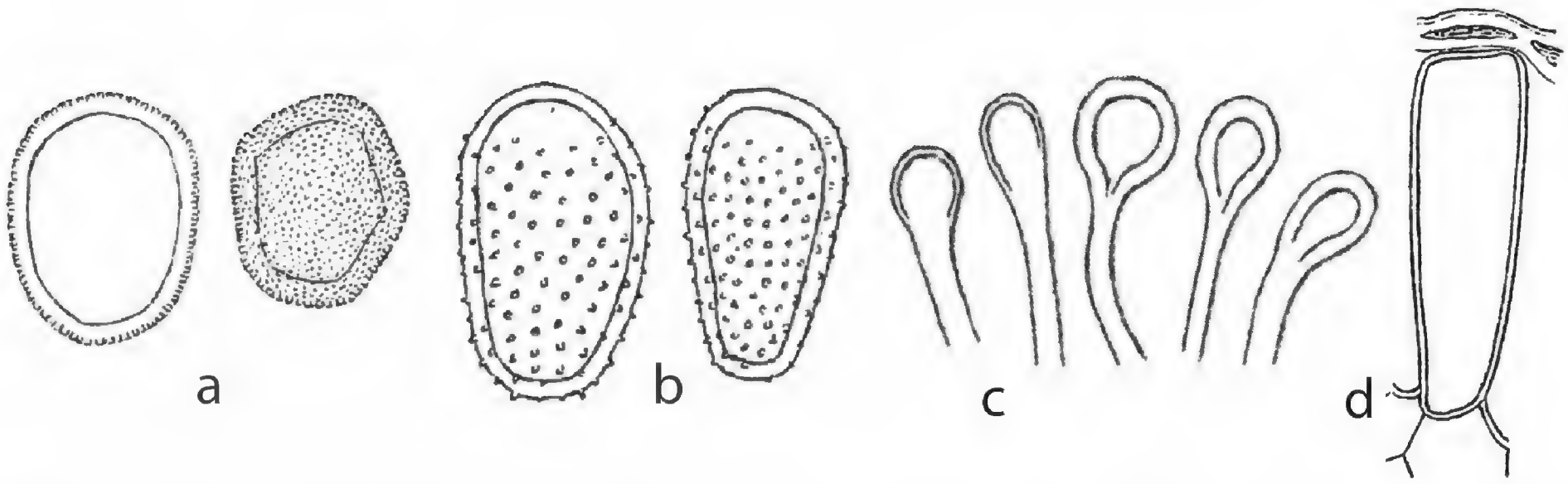


Figure 27. *Melampsora amygdalinae* on *Salix triandra*: **a.** Aeciospores; **b.** Urediniospores with smooth apex, spore wall evenly thick; **c.** Paraphyses with evenly thick walls; **d.** Teliospore from subepidermal crust, spore wall evenly thick; (**a–d** from Klebahn 1914: 782).

Spermatogonia subcuticular, barely projecting, 100 µm in diam. – **Aecia** on young twigs and leaves, usually hypophyllous, 1 mm in diam., reaching 10 mm in length in groups on the twigs, confluent, bright orange. – **Aeciospores** round to ovoid to angular, formed in chains with small intercalary cells, 18–23 × 14–19 µm; wall 2 µm thick, finely verrucose (approx. 4 warts/µm²). – **Uredinia** hypophyllous, scattered, small (0.5 mm in diam.), bright orange, producing pale spots on the upper side of the leaves. Paraphyses 30–50 µm long, capitate (head 10–18 µm in diam.) or clavate; wall thickness even, 1–3 µm. – **Urediniospores** elongated, obovoid to clavate, 19–32 × 11–15 µm; wall 1.5 µm thick, distantly echinulate (approx. 0.30 spines/µm²), with smooth apex. – **Telia** hypophyllous, rarely epiphyllous, subepidermal, small (0.3–0.5 mm), single or in groups, often spread over the whole leaf. – **Teliospores** irregular, prismatic, rounded at both ends, 18–42 × 7–14 µm; wall thickness even, 1 µm. – Reference: Helfer (1992: 128).

Remarks. *Melampsora amygdalinae* is the only autoecious rust on *Salix*. It also seems to be the only rust together with *M. vitellinae* causing serious damage to its host in natural and cultivated populations, and it makes the stems of affected willows useless for basket work (Peace 1962; Buczacki and Harris 1981; Phillips and Burdekin 1982; Smith et al. 1988; Helfer 1992). – For records of *M. amygdalinae* in Austria see Poelt and Zwetko (1997: 75).

(4) *Melampsora ari-salicina* A. Raabe

Probably hetereu-form:

(0,I on: *Arum maculatum*)

(II,III on: *Salix fragilis*)

Spermatogonia, **aecia** and **telia** as in *M. allii-fragilis*. – **Urediniospores** larger (36–40 × 19–22 µm). – References: Raabe (1938: 39), Gäumann (1959: 160).

Remarks. *Melampsora ari-salicina* has been described by Raabe (1938) as a provisional species from SW Germany, but the description of this taxon is insufficient. Aecia on *Arum maculatum* and telia on *Salix fragilis* have been found at the same location. One inoculation experiment with these aecia showed positive results on *S. fragilis*, another experiment was not successful. *Melampsora ari-salicina* might occur in Austria, too.

5–14 *Melampsora epitea* s.l. (*M. epitea* complex)

5 *Melampsora epitea* s.l.

= *Melampsora epitea* Thüm. (s. Hylander et al. 1953)

= *Melampsora epitea* Thüm. var. *epitea* (e.g., s. Wilson and Henderson 1966)

= *Melampsora epitea* Thüm. var. *reticulatae* (A. Blytt) Jørst. (l.c.)

Accepted species within the complex: ***M. abietis-caprearum***, ***M. arctica*** (syn. *M. alpina*), ***M. euonymi-caprearum***, ***M. lapponum***, ***M. laricis-epitea***, ***M. repentis***, ***M. reticulatae***, ***M. ribis-epitea***, ***M. ribis-purpureae***

Hetereu-forms, forms with facultative host alternation and hemi-forms:

0,I on: *Abies alba*, *Dactylorhiza majalis*, *Euonymus europaeus*, *Larix decidua*, *Neotinea ustulata* [syn. *Orchis u.*], *Ophrys sphegodes*, *Orchis mascula*, *Ribes alpinum*, *R. uva-crispa* agg., *Saxifraga aizoides*, *S. androsacea*, *S. biflora* × *oppositifolia*, *S. blepharophylla*, *S. exarata*, *S. moschata*?, *S. oppositifolia*, (*Abies cephalonica*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*, *Anacamptis morio* [syn. *Orchis m.*], *Dactylorhiza incarnata*, *D. maculata*, *D. sambucina*, *D. traunsteineri*, *Epipactis helleborine*, *Euonymus latifolius*?, *E. verrucosus*?, *Gymnadenia conopsea*, *Larix kaempferi*, *Neottia ovata* [syn. *Listera o.*], *Ophrys insectifera*, *Orchis militaris*, *O. purpurea*, *Platanthera bifolia*, *P. chlorantha*, *Pseudorchis albida*, *Ribes aureum*, *R. nigrum*, *R. rubrum*, *R. sanguineum*, *R. spicatum*, *R. uva-crispa*, *R. uva-crispa* subsp. *grossularia*, *Saxifraga adscendens*, *S. cernua*, *S. moschata*, *S. muscoides*?)

(0?,I on: *Viola palustris*)

II,III on: *Salix alpina*, *S. appendiculata*?, *S. arbuscula* agg., *S. aurita*?, *S. caprea*, *S. cinerea*, *S. daphnoides*, *S. eleagnos*, *S. glabra*, *S. helvetica*, *S. herbacea*,

S. myrsinifolia, *S. nigricans* agg., *S. purpurea*, *S. repens*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, *S. waldsteiniana*, (*S. appendiculata*, *S. aurita*, *S. bicolor*, *S. caesia*, *S.* ×*calodendron*, *S.* ×*dasyclados*, *S. foetida*, *S. fragilis*, *S. hastata*, *S. hegetschweileri*, *S. myrsinites* agg., *S. myrtilloides*, *S. pentandra*, *S. purpurea* × *viminalis*, *S. repens* subsp. *rosmarinifolia*, *S.* ×*stipularis*?, *S. triandra*, *S. viminalis*)

II,([III]) on: *Salix* ×*smithiana*?, *S. viminalis* – less susceptible hosts

The following records cannot be assigned to any species within the *M. epitea* complex:

(II,III on: *Salix alba*, *S. aurita* × *repens*, *S. glaucosericea*, *S. glaucosericea* × *myrsinifolia*, *S. hastata* × *herbacea*, *S. hastata* × *myrsinifolia*)

The species complex of *Melampsora epitea* s.l. is characterised by extremely uniform thin-walled subepidermal teliospores which are not thickened at the apex and have no distinguishable pore; the urediniospores are globoid or ovoid with uniformly echinulate walls. The heads of the inner uredinial paraphyses are comparatively small and mostly thick-walled; the peripheral paraphyses are normally thin-walled, more clavate and generally larger than the more distinctly capitate inner ones (Jørstad 1940; Wilson and Henderson 1966). Shape and size of uredinial paraphyses are not always uniform within one rust collection. Nevertheless, Jørstad (1940) and Wilson and Henderson (1966) recognised two varieties within *M. epitea* s.l.: *M. epitea* var. *reticulatae* differs from var. *epitea* in its larger urediniospores (24–32 × 16–22.5 µm) and larger uredinial paraphyses (up to 90 µm long, with 25–35 µm wide head and up to 10 µm thick wall).

In Great Britain, only seven species of *Melampsora* on willows have been recorded by Wilson and Henderson (1966). In contrast, 17 species have been recorded by Gäumann (1959) in Central Europe. Klebahn (1914) and Gäumann (1959) have demonstrated that 'cryptic' species within the *M. epitea* complex are separable. Based on inoculations of aecial hosts and urediniospore morphology, Gäumann identified at least eight species within the complex, but not all species examined differ in urediniospore morphology. Due to their difficult identification and often overlapping *Salix* host range, most of the species cannot be recognised solely from their occurrence on a particular *Salix* host, but each has a distinctive host specialisation pattern in both aecial and telial stage. Jørstad (1940) and Henderson (1957) have emphasised that classification should be based on morphological characters as far as possible. But they have found only few characters for segregating taxa within the *M. epitea* group. The only morphological character that has been extensively used by Jørstad (1940, 1953) and Henderson (1957) is the dimension of the ± capitate uredinial paraphyses. Nevertheless, most collections on British willows were grouped according to their aecial hosts by Wilson and Henderson (1966). Parmelee (1989) has emphasised that *M. epitea*, as treated in his paper, certainly contains more than one species, but until abundant cross-inoculations can be made and combined with detailed measurements, a realistic treatment of American collections is impossible.

Helfer (1992) proved that differences in urediniospore spine density (Fig. 28, p. 216) help to characterise rust species within the *Melampsora epitea* complex and to distinguish them from *M. farinosa*: Only urediniospores in collections of *M. alpina* (now *M. arctica*) have significantly greater spine density (0.9 spines/µm²) than those of other willow rusts. The collections of *M. ribis-epitea* and *M. farinosa* have urediniospores with significantly lower spine density (0.3 spines/µm²). Most other species (e.g., *M. abietis-caprearum*, *M. ribis-purpureae*, *M. laricis-epitea*, *M. euonymi-caprearum*, *M. repentis* and *M. reticulatae*) have urediniospores with intermediate, overlapping spine densities (0.4–0.6 spines/µm²). As pointed out under *M. abietis-caprearum*, urediniospore spine distances reported by Gäumann (1959) and spine densities measured by Helfer (1992) show discrepancies. This can be seen as well in *M. ribis-epitea* and *M. repentis*.

DNA sequence data, where available, support morphological and biological data, the latter being based on cross-inoculations. Smith et al. (2004) compared sequences from internal transcribed spacer (ITS) regions of rDNA, which were obtained from urediniospores of *Melampsora epitea* (s.l.). Rust samples were taken from four *Salix* species at different locations in N America. The phylogenetic analysis of nuclear ribosomal ITS regions indicates that *M. epitea* samples from arctic and temperate hosts in N America are divergent, perhaps in part because all rusts examined diverge according to host species. Moreover, the analysis provides evidence that arctic samples from N America are more closely related to arctic samples from Europe than to temperate samples from N America. Arctic samples were taken from *Salix arctica* at four locations in Canada; rust samples on three other *Salix* species were collected in Minnesota (USA). The urediniospores of *M. epitea* on *Salix arctica* have significantly greater spine density than those on the three other *Salix* species. The studies of Smith et al. (2004) have revealed substantial molecular divergence of *M. epitea* at the host species level. *Melampsora epitea* from arctic willow represents a distinct clade and is easily distinguished from *M. epitea* from temperate hosts in N America. This is not the first report of differentiating seemingly similar forms of rusts on willow. Pei and Ruiz (2000) have separated the form of *Melampsora* that causes stem cankers on *Salix viminalis* in Britain from the leaf-infecting form by molecular comparisons.

Hurtado and Ramstedt (2002) compared genetic variation among four geographically defined populations of *Melampsora epitea* (s.l.). A two-primer combination was used for AFLP fingerprinting of isolates from Northern Ireland, Sweden, France and Chile. Geographical distance among the pathogen populations correlates poorly with genetic distance. The rust isolates in this study group more with the willow species on which they were found than with country of origin. However, the study includes too few willow species other than *Salix viminalis* to confirm this conclusion.

Key to the Melampsora species on *Salix*

(*M. ari-salicina* is not included because its description is insufficient)

1a Urediniospores elongate; wall echinulate at sides, but smooth at apex 2
1b Urediniospores roundish, (broadly) ellipsoid to globoid; wall evenly echinulate 4
2a Telia mainly epiphyllous, subcuticular. Wall of urediniospores rather thick (3 µm and more) ..... *M. allii-fragilis*, *M. galanthi-fragilis*
2b Telia amphigenous or hypophyllous, subepidermal. Wall of urediniospores about 1.5–2 µm thick 3
3a Telia amphigenous. Urediniospores 20–36 × 11–17 µm; wall about 2 µm thick ..... *M. vitellinae*
3b Telia hypophyllous. Urediniospores 19–32 × 11–15 µm; wall 1.5 µm thick ..... *M. amygdalinae*
3c Telia hypophyllous. Urediniospores longer, 26–44 × 12–16 µm; wall about 2 µm thick ..... *M. laricis-pentandrae*
4a Telia epiphyllous, subcuticular 5
4b Telia epiphyllous, subepidermal (see **Note 1** below) ..... (*M. epitea* s.l.) *M. lapponum*
4c Telia mainly hypophyllous, subepidermal (see **Note 1** below) ..... (*M. epitea* s.l.) 6
5a Teliospore wall pronouncedly thickened at the apex, up to 10 µm (see **Note 2** below) ..... *M. farinosa*
5b Teliospore wall uniformly thin, about 1 µm (see **Note 2** below) ..... *M. ribis-viminalis*
6a Urediniospores rather large (17–35 × 15–23 µm). Uredinial paraphyses rather long (60–95 µm), head 18–41 µm wide ..... (*M. epitea* var. *reticulatae*) *M. reticulatae*
6b Urediniospores smaller (12–25 × 9–19 µm). Uredinial paraphyses shorter (30–80 µm), head 15–25 µm wide ..... (*M. epitea* var. *epitea*) 7
7a Uredinia mainly epiphyllous. Wall of urediniospores very densely echinulate (0.9 spines/µm²) ..... *M. arctica*
7b Uredinia amphigenous or hypophyllous. Wall of urediniospores less densely echinulate (0.6–0.3 spines/µm²) 8
8a Wall of urediniospores about 1.5 µm thick 9
8b Wall of urediniospores (2–)2.5–3.5 µm thick 10
9a Uredinial paraphyses 30–40 µm long and thin-walled (1.5–3 µm thick). Wall of urediniospores moderately densely echinulate, 0.6 spines/µm² (see **Note 3** below) ..... *M. abietis-caprearum*
9b Uredinial paraphyses 40–70 µm long with slightly thicker walls (2–5 µm). Wall of urediniospores moderately densely echinulate, 0.5 spines/µm² (see **Note 3** below) ..... *M. repentis*
10a Uredinial paraphyses with apically thickened walls (up to 5–10 µm) 11
10b Wall thickness of uredinial paraphyses even (1.5–4 µm) 12
11a Urediniospores mainly globoid, rarely elongate, 14–19 × 14–17 µm; wall thickened (up to 4 µm) with thin areas ..... *M. euonymi-caprearum*
11b Urediniospores mainly obovoid, slightly elongate, 12–25 × 9–19 µm; wall up to 2.5–3.5 µm thick but without thin areas ..... *M. laricis-epitea*
12a Wall of urediniospores about 2.5 µm thick with thin areas, moderately densely echinulate (0.6 spines/µm²) ..... *M. ribis-purpureae*
12b Wall of urediniospores 3–3.5 µm thick with thin areas, distantly echinulate (0.3 spines/µm²) ..... *Melampsora ribis-epitea*

Note 1: Telia of *Melampsora reticulatae* (*M. epitea* var. *reticulatae*) are mainly epiphyllous. *M. lapponum* is best characterised by the comparatively large and thin-walled heads of the uredinial paraphyses. In specimens of *M. reticulatae* on *Salix reticulata* the walls of the paraphyses are apically thickened up to 10 µm, but Jørstad (1940, 1953) also assigned specimens on other *Salix* hosts to *M. epitea* var. *reticulatae*. The walls of their uredinial paraphyses are apically thickened up to 5 µm. These thin-walled forms from N Norway resemble *M. lapponum* considerably.

Note 2: *Melampsora farinosa* and *M. ribis-viminalis* have ellipsoid or globoid urediniospores with evenly echinulate walls. Because of overlapping *Salix* host ranges, they can be confused with species of the *M. epitea* complex: Although frequently occurring in Austria, rusts on *Salix caprea*, *S. appendiculata* and related species are insufficiently known. The differentiation between *M. farinosa* and species of the *M. epitea* complex (especially *M. euonymi-caprearum*, *M. ribis-epitea* and *M. laricis-epitea*) causes problems when only uredinia are present. In order to know more about the distribution in the area, it needs sampling of both the uredinial and telial state (Poelt and Zwetko 1997). In the uredinial stage, the identification of another species, *M. ribis-viminalis*, is rather difficult. For the rusts on *Salix caprea* and *S. viminalis* special keys are presented; see under *M. farinosa* (p. 233) and under *M. ribis-viminalis* (p. 243).

Note 3: Spine densities reported by Helfer (1992) and spine distances reported by Gäumann (1959) show some discrepancy. In collections of *Melampsora abietis-caprearum* from Austria the spine distance was always 2 µm.

6 *Melampsora abietis-caprearum* Tubeuf

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. arctica* Rostr. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *abietis-caprearum* (Tubeuf) Bagyanarayana

Hetereu-form:

0,I on: *Abies alba*, (*A. cephalonica*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)

II,III on: *Salix caprea*, *S. myrsinifolia*, (*S. appendiculata*, *S. aurita*, *S. cinerea*, *S. eleagnos*, *S. purpurea*, *S. repens*, *S.* ×*stipularis*?)

II,([III]) on: *Salix viminalis*, (*S. foetida*, *S. helvetica*) – less susceptible hosts

Spermatogonia subepidermal, equally frequent on both sides of the youngest needles, 70–150 µm in diam., 50–60 µm high. – **Aecia** hypophyllous, bright yellow, 0.5–0.7 mm in diam., frequently extended to lines (up to 10 mm long). – **Aeciospores** globoid, 14–17(–19) µm in diam., or ellipsoid, 19–21 × 12–14 µm; wall 1.5 µm thick, densely verrucose (approx. 4 warts/µm²), distance of warts approx. 1 µm. – **Uredinia** hypophyllous, irregularly scattered, on small yellow spots, pulverulent, soon naked, small, 0.5 mm in diam. Paraphyses numerous, clavate (or capitate), 30–40 µm long, swollen upper part of paraphyses 16–24 µm wide, basal part 4–5 µm; wall thickness 1.5–3(–3.5) µm. – **Urediniospores** globoid (to broadly obovoid), 13–15 µm in diam., rarely ellipsoid or broadly pyriform, 16–19 × 12–14 µm; wall evenly thick (approx. 1.5 µm), densely echinulate (approx. 0.6 spines/µm²); spines small. – **Telia** hypophyllous, subepidermal, irregular, ± confluent forming black crusts. – **Teliospores** light brown, long-elliptical or ± prismatic, 19–30 × 9–12 µm; wall thickness even, approx. 1 µm. – References: Gäumann (1959: 145–146), Helfer (1992: 127).

Remarks. Gäumann (1959) described the urediniospore ornamentation of *Melampsora abietis-caprearum* as 'very densely echinulate-verrucose; warts very small; distance of warts 1 µm or less'. Our examination of the rust collections from Austria did not confirm Gäumann's description. We could not observe ornaments intermediate between spines and warts; the spine distance was always about 2 µm.

Morphologically this rust was distinguished from the other species of the *Melampsora epitea* complex and from *M. farinosa* by its rather small, thin-walled urediniospores and thin-walled uredinial paraphyses. Helfer (1992) has used differences in urediniospore spine density to characterise willow rusts. But often he found the differences to be rather small. Only urediniospores in collections of *M. alpina* (= *M. arctica*) have significantly greater spine density (0.9 spines/µm²) than those of collections of other willow rusts. The collections of *M. ribis-epitea* and *M. farinosa* have urediniospores with significantly lower spine density (0.3 spines/µm²). Most other species (e.g., *M. abietis-caprearum*, *M. ribis-purpureae*, *M. laricis-epitea*, *M. euonymi-caprearum*, *M. repentis*, *M. reticulatae* and *M. ribis-viminalis*) have urediniospores with intermediate, overlapping spine densities (0.6–0.4 spines/µm²; see Fig. 28, p. 216). Urediniospore spine distances in *M. abietis-caprearum* reported by Gäumann (1959) are not in accordance with spine densities measured by Helfer (1992) and by ourselves. While Gäumann (l.c.) reports 1 µm distance for *M. abietis-caprearum*, and 2 µm for *M. laricis-epitea*, we find 2 µm distance in both species. Helfer (l.c.) presents very similar spine densities (0.6 spines/µm² in *M. abietis-caprearum*, and 0.55 in *M. laricis-epitea*).

In Austria, *Melampsora abietis-caprearum* is a rare rust; only one collection on the aecial host and few collections on the uredinal and telial hosts are reported. In the uredinial stage, the assignment of the samples to this species has been done on the basis of thin-walled paraphyses and spores. To our knowledge no evidence is provided for the occurrence of *M. abietis-caprearum* on *Salix appendiculata* in Austria; the corresponding information in Zwetko (2000) is erroneous. – For records of *M. abietis-caprearum* in Austria see Poelt and Zwetko (1997: 74–75).

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

7 *Melampsora arctica* Rostr.

Figs 28a, 29

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. arctica* Rostr. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *arctica* (Rostr.) Bagyanarayana; *M. alpina* Juel

Hetereu-form:

0,I on: *Saxifraga androsacea*, *S. biflora* × *oppositifolia*, *S. blepharophylla*, *S. exarata*, *S. oppositifolia*, (*S. adscendens*, *S. aizoides*?, *S. cernua*, *S. moschata*)

II,III on: *Salix herbacea*, (*S. myrsinites* agg., *S. retusa*)

Spermatogonia epiphyllous, subepidermal, orange, 150–160 µm in diam., 90–130 µm high. – **Aecia** single, epiphyllous, bright orange, 0.3–0.6 mm wide, occasionally surrounded by pseudoparenchymatic cells reminiscent of primitive paraphyses. – **Aeciospores** globoid to broadly ovoid to slightly angular, 16–27 × 13–24 µm; wall hyaline, 1.5–3 µm thick, very finely verrucose; distance of warts less than 1 µm (>1.2 warts/µm²). – **Uredinia** amphigenous, but mainly epiphyllous, 0.5–1 mm in diam., single, bright orange when young, later brown. Paraphyses numerous, capitate, 40–60 µm long, head 17–22 µm wide; wall thickness even, 4–6 µm. – **Urediniospores** globoid, broadly obovoid or ellipsoid, 14–20 × 11–16 µm; wall hyaline, 1.5–2 µm thick, echinulate with dense, fine spines (Fig. 28a, p. 216); spine distance (1–)1.4(–2) µm (0.9 spines/µm²). – **Telia** mainly hypophyllous opposite the uredinia, subepidermal, 0.5 mm in diam., single or confluent, forming small crusts, at first brown, later blackish. – **Teliospores** clavate or prismatic, rounded or slightly pointed, 23–50 × 6–l7 µm; wall pale

Figure 28. *Melampsora*, comparison of urediniospore ornamentation in SEM: **a.** *Melampsora arctica*, spines rather densely arranged; **b.** *M. farinosa*, spines less densely arranged as in *M. arctica*; **c.** *M. laricis-epitea* f.sp. *laricis-retusae*; the spines in c are intermediate between **a** and **b** in density; (**a–c** by Paul Blanz).

yellowish or brownish; wall ± evenly 1 µm thick, occasionally slightly thickened at the apex; apical pore visible when germinating. – **Basidiospores** 8–10 × 6–8 µm, with brownish-red content. – References: Gäumann (1959: 170–171), Helfer (1992: 128).

Remarks. Collections of rust on *Salix arctica* from arctic N America and Greenland have been designated as *Melampsora arctica* and rust on *Salix herbacea* from Europe as *M. alpina*. Both taxa have been listed as synonyms of *M. epitea* s.l. The species complex of *M. epitea* might represent one of the most diverse and confusing groups of rust fungi. At least two taxa within the complex alternate between *Saxifraga* and *Salix*, each has a distinctive host specialisation pattern in both aecial and telial stage. Previous workers have found only few morphological characters for segregating taxa within the complex. From examination of uredinial paraphyses of the collections on mountain willows in Scotland, it was evident that the collections fall into two major groups. The small-headed type predominates on *Salix herbacea*, *S. herbacea* × *myrsinites*, *S. myrsinites* and *S. lapponum*, whilst the large-headed type occurs on *Salix reticulata* and *S. lanata* (Henderson 1957). Jørstad (1940) recognised two varieties within the *M. epitea* complex; *M. epitea* var. *reticulatae* (= *M. reticulatae*) differs from var. *epitea* in its larger urediniospores (24–32 × 16–22.5 µm) and larger uredinial paraphyses, up to 90 µm long, with head 25–35 µm wide and wall 10 µm thick (Wilson and Henderson 1966). The only morphological character that has been extensively used by Jørstad (1940, 1953) and Henderson (1957) is the dimension of the ± capitate uredinial paraphyses. Jørstad (1953) has noticed that the two varieties are not sharply delimited and that intermediates occur.

Henderson (1953) used cross-inoculations to investigate the relation between rust morphology and host specificity. He showed that *M. epitea* var. *epitea* typically alternates between *Salix herbacea* and *Saxifraga hypnoides* and that var. *reticulatae* alternates between *Salix reticulata* and *Saxifraga aizoides*. Urediniospores found on *Salix herbacea* were used to inoculate *Salix herbacea*, *S. lanata*, *S. repens*, *S. reticulata* and *S.* ×*sadleri*. Only *Salix herbacea* became infected. From the same Scottish locality urediniospores on *Salix reticulata* were used to inoculate *Salix herbacea*, *S. lanata*, *S. repens*, *S. reticulata* and *S.* ×*sadleri*. Only *Salix reticulata* became infected. The results from the inoculation experiments show that the rusts on *Salix herbacea* and *S. reticulata* are strictly specialised. This is in agreement with results from previous experiments (e.g., Jacky 1899; Klebahn 1908).

Helfer (1992) and Smith et al. (2004) show that morphological differences in urediniospore spine characteristics can be useful for segregating taxa within the complex. Urediniospores in collections of *Melampsora epitea* on *Salix arctica* have greater spine density than those of collections on other willow species in N America. Urediniospores in collections of *M. alpina* (= *M. arctica*) have significantly greater spine density than those of collections of other willow rusts in Europe. The similarity of scanning electron micrographs of urediniospores from *M. epitea* on *Salix arctica* (see Smith et al. 2004) and *M. epitea* on *Salix herbacea* (see Helfer 1992) is conspicuous. Judging from the micrographs, it is doubtful if the urediniospores of both rusts are distinguishable. However, the mean values for spine density given by Helfer (1992) differ from those given by Smith et al. (2004). In collections of *M. epitea* s.l. from Europe the spine density ranges between 0.3–0.9 spines/µm² (Helfer 1992). In most European collections the mean values vary between 0.45–0.6 spines/µm². In *M. alpina* (= *M. arctica*) urediniospores have been found to have significantly greater spine density (0.9 spines/µm²). In *M. ribis-epitea*, urediniospores show significantly lower spine density (0.3 spines/µm²). In contrast, in collections of *M. epitea* from N America the spine density ranges between 0.20–0.44 spines/µm² (Smith et al. 2004); the latter authors found the urediniospores of *M. epitea* on *Salix arctica* to have significantly greater spine density (0.44 spines/µm²) than those on three *Salix* species from temperate N America. The differences between the mean values for spine density given by Helfer (1992) and Smith et al. (2004) are high. However, the former author used SEM while the latter authors studied the spores by light microscopy. It must be considered that these methods do not necessarily lead to the same results. Littlefield and Schimming (1989) point out the influence on size and shape of urediniospores by relative ambient humidity.

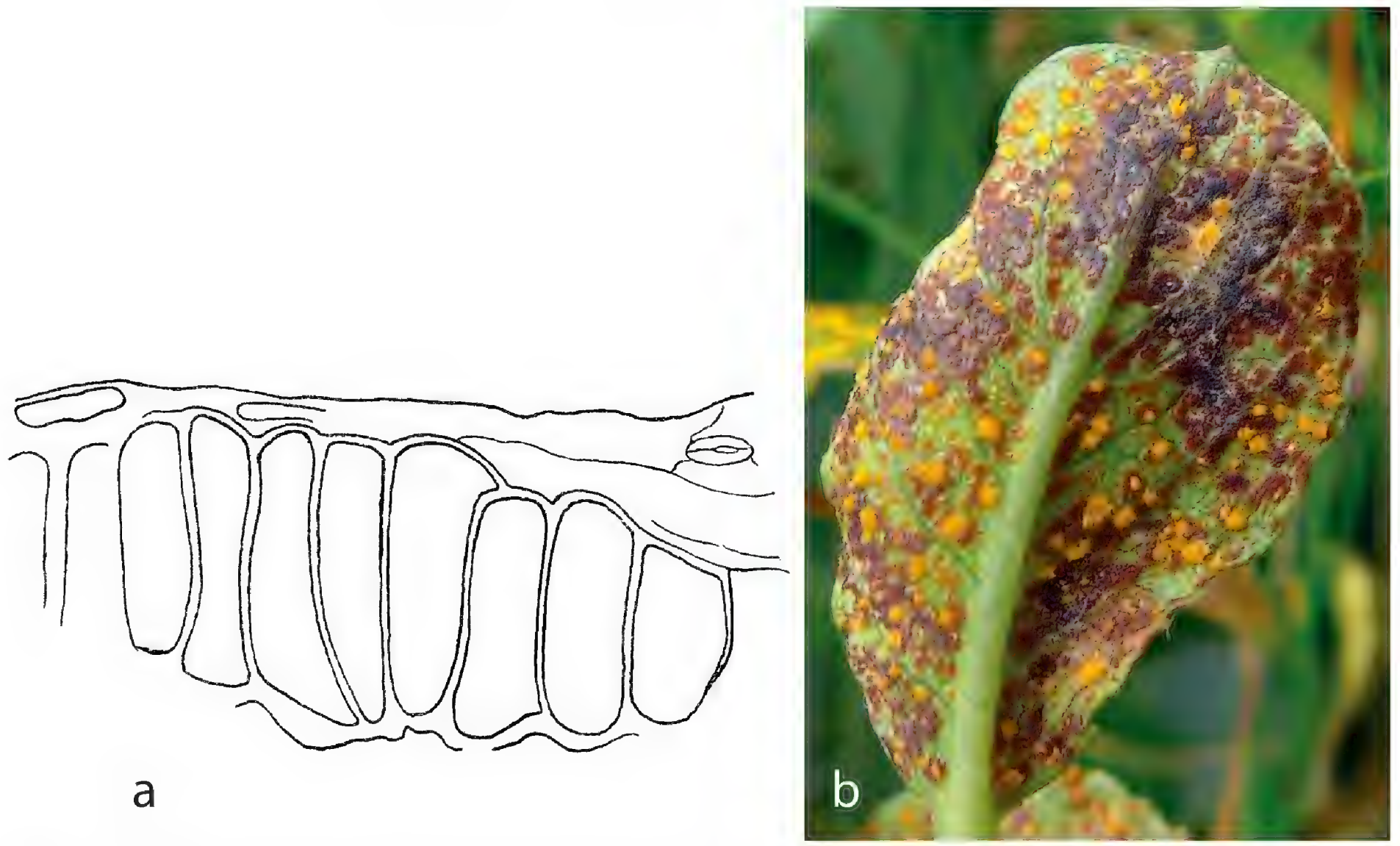


Figure 29. *Melampsora arctica*. **a.** On *Salix herbacea*, teliospores arranged in subepidermal crust; **b.** *M.* cf. *arctica* on *Salix retusa*, hypophyllous uredinia and telia (**a** from Fischer 1904: 491, as *M. alpina*, with permission from Bryolich; **b** by Julia Kruse).

When comparing *Melampsora arctica* on *Salix herbacea* from N Scandinavia with those from the Austrian Alps, we found like Helfer (1992) that both share a very high spine density (see Fig. 28a, p. 216), which separates them clearly from other *Melampsora* species.

Smith et al. (2004) compared morphological characters and sequences from internal transcribed spacer (ITS) regions of rDNA, which were obtained from urediniospores of *Melampsora epitea* s.l. Rust samples were taken from four *Salix* species in different locations in N America. Their phylogenetic analysis of nuclear ribosomal ITS regions indicates that *M. epitea* samples from arctic N America are more closely related to arctic samples from Europe (Sweden) than to temperate samples from N America. The results from ITS sequence comparisons show that *M. epitea* from arctic willow (*Salix arctica*) represent a distinct clade and are easily distinguished from *M. epitea* on temperate willow species in N America.

Melampsora arctica shows a probably circumpolar, arctic-alpine distribution (Europe, Asia, Greenland and N America). – Aecia of *M. alpina* (= *M. arctica*) on *Saxifraga moschata* have been reported from the Pyrenees (Mayor 1970). Aecia found on *Saxifraga moschata* in Austria probably belong to *M. reticulatae*; they occur in close vicinity to *Salix reticulata*. However, Gäumann (1959) noted that the host-parasite alternation *Saxifraga moschata-Salix reticulata* has not been proven experimentally. – From the European Alps two rust species are reported on *Salix herbacea*: *M. arctica* and *M. laricis-epitea* f.sp. *laricis-retusae*. The urediniospores of the latter are 18–22 µm long and 14–18 µm wide, with 2 µm wall thickness and 2 µm spine distance. In *M. arctica* the spore size is slightly smaller and spine distance shorter (see above). Henderson (2004) reported two rust species on *Salix herbacea* from the British Isles: *M. arctica* and *M. epitea* s.l. The host alternation of the latter is unknown, and its urediniospores are less densely echinulate than those of the former species. Jørstad (1951) supposed that *Salix herbacea* may serve as host for *M. epitea* var. *reticulatae* (= *M. reticulatae*) in Iceland, and Gjærum (1974) confirmed this supposition. – For the distribution of *M. arctica* in Austria see Poelt and Zwetko (1997: 76).

8 *Melampsora euonymi-caprearum* Kleb.

Fig. 30

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. epitea* Thüm. f.sp. *euonymi-caprearum* (Kleb.) Boerema & Verh.; *M. evonymi-caprearum* Kleb. (orthogr. var.)

Hetereu-form:

0,I on: *Euonymus europaeus*, (*E. latifolius*?, *E. verrucosus*?)

II,III on: *Salix aurita*?, *S. caprea*, *S. cinerea*?, (*S. eleagnos*)

II on: *Salix* ×*smithiana*?

Spermatogonia subepidermal, 200 µm in diam., 80 µm high. – **Aecia** in groups, mainly hypophyllous, bright orange, in groups, up to 1.5 mm in size. – **Aeciospores** mainly ovoid, 18–23 × 14–19 µm; wall up to 5 µm thick, but with some distinctly thinner spots (probably marking germ pores), finely verrucose (approx. 4 warts/µm²).

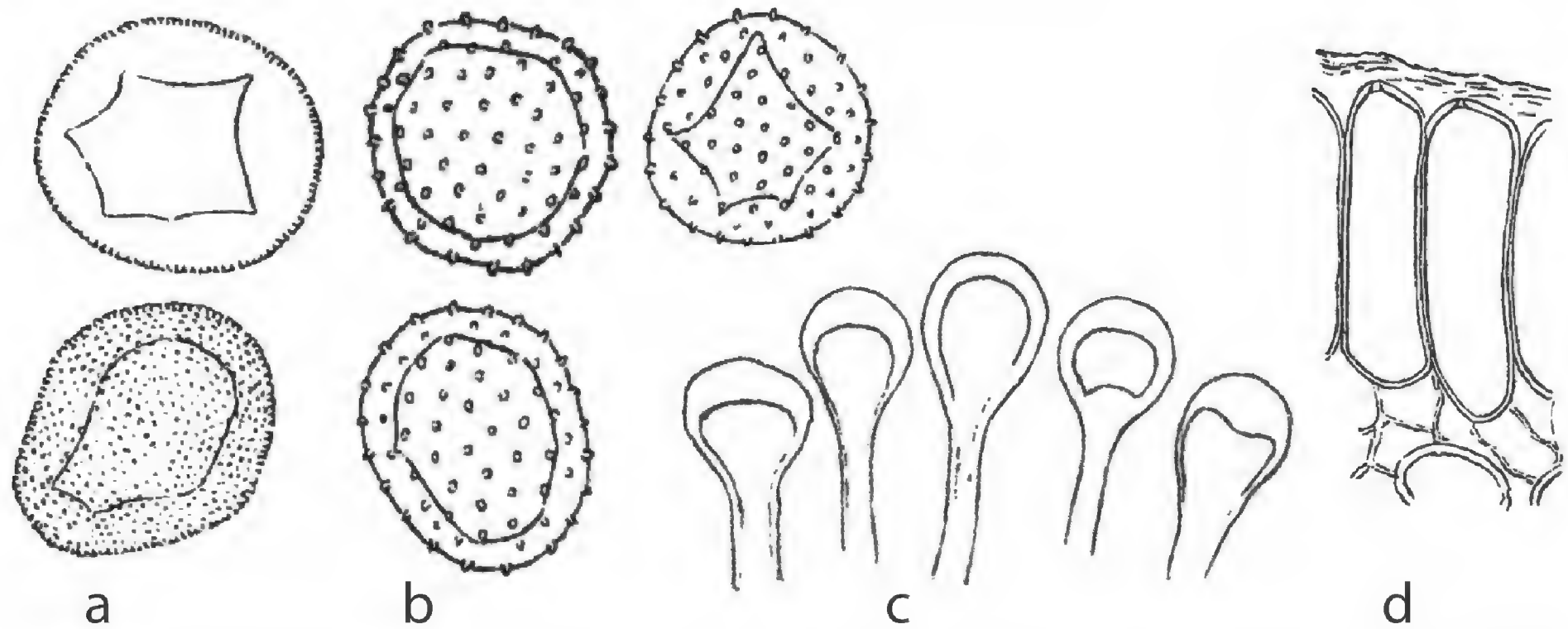


Figure 30. *Melampsora euonymi-caprearum*. **a.** On *Euonymus europaeus*: aeciospores rather thick-walled with some distinctly thinner spots; **b–d.** On *Salix cinerea*: **b.** Urediniospores with similar wall thickenings; **c.** Paraphyses; **d.** Teliospores; (**a–d** from Klebahn 1914: 794).

– **Uredinia** hypophyllous in leaf spots, single or in clusters, small (0.5 mm in diam.). Paraphyses mainly capitate 50–70 × 18–25 µm; wall up to 8 µm thick at the apex, 2 µm elsewhere. – **Urediniospores** mainly globoid, rarely elongate, 14–19 × 14–17 µm; wall either thin (1.5 µm) or thickened (up to 4 µm) between narrow thinner areas, moderately densely echinulate (0.5 spines/µm²). – **Telia** hypophyllous, subepidermal, small (0.5 mm), in groups. – **Teliospores** irregular, prismatic, rounded at both ends, 25–40 × 7–13 µm; wall thickness ± even, 1 µm. – Reference: Helfer (1992: 129).

Melampsora euonymi-caprearum is reported to show two specialised forms (Klebahn 1904; Mayor 1927; Gäumann 1959):

- f.sp. *typica* Kleb. on *Salix caprea* and *S. cinerea*,
- f.sp. *euonymi-incanae* Schneid.-Or. on *S. eleagnos*.

Remarks. *Melampsora euonymi-caprearum* f.sp. *euonymi-incanae* is reported from Switzerland (Mayor 1958) and France (Dupias 1967). This form has aeciospores with thinner walls than f.sp. *typica*. Its uredinial paraphyses are rarely thickened at the apex. – For records of *M. euonymi-caprearum* in Austria see Poelt and Zwetko (1997: 78).

(9) *Melampsora lapponum* Lindf.

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. epitea* Thüm. f.sp. *lapponum* (Lindf.) Bagyanarayana

Hetereu-form:

(0?,I on: *Viola palustris*)

(II,III on: *Salix lapponum*)

Spermatogonia unknown. – **Aecia** in groups, hypophyllous or rarely epiphyllous, orange. – **Aeciospores** ellipsoid or globoid, 19–27 × 18–20 µm; wall up to 3 µm thick, hyaline, finely and densely verrucose; distance of warts less than 1 µm; contents yellow. – **Uredinia** hypophyllous, minute, 0.5 mm in diam., yellow-orange. Inner paraphyses capitate, head 15–30 µm in diam.; wall 1–4 µm thick; outer paraphyses clavate, small and thin-walled. – **Urediniospores** globoid, ellipsoid or somewhat polyhedral, 20–21 × 15–16 µm; wall echinulate; contents yellow. – **Telia** epiphyllous, subepidermal, small (0.25–0.5 mm in diam.), orange-brown, then dark brown. – **Teliospores** prismatic, rounded at both ends, 30–50 × 6–12 µm; wall brown; wall thickness even, 1 µm. – Reference: Gäumann (1959: 164).

Remarks. *Melampsora lapponum* has been described from Scandinavia and recognised as a separate species by Hylander et al. (1953), while Gjærum (1974) listed it as specialised form under *M. epitea* var. *epitea*. Because of the large, although usually more thin-walled uredinial paraphyses, *M. lapponum* particularly resembles *M. reticulatae* (Jørstad 1953, as *M. epitea* var. *reticulatae*). *Melampsora lapponum* is best characterised by the comparatively large and thin-walled heads of the uredinial paraphyses (Jørstad 1940). In specimens from N Norway, they are up to 27 µm wide with walls up to 4 µm thick. In specimens of *M. epitea* var. *reticulatae* on *Salix reticulata* the walls of the paraphyses are apically thickened up to 10 µm, but Jørstad (1940, 1953) also assigned specimens on other *Salix* hosts to *M. epitea* var. *reticulatae*. The walls of their uredinial paraphyses are apically thickened up to 7–8 µm, 6 µm, or 5 µm. Some of the more thin-walled forms from N Norway possibly belong to *M. lapponum*.

Based on Helfer (1992), Pei (2005) described the spine density on the surface of urediniospores in *M. lapponum* as considerably higher than that of other willow rusts recorded in Britain. It appears to be an error because Helfer (1992) neither recorded *M. lapponum*, nor examined specimens of this taxon. He listed *Salix lapponum* only as host of *M. laricis-epitea*.

The occurrence of *M. lapponum* in Moravia raises questions (see Gäumann 1959). Denchev (1995) recorded *M. lapponum* from Bulgaria. In Austria, *M. lapponum* might occur on *Salix helvetica* (*S. lapponum* agg.); it has not been listed in the Austrian rust catalogue (Poelt and Zwetko 1997).

10 *Melampsora laricis-epitea* Kleb.

Figs 23, 28c, 31, 32b, c, 33, 34

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. epitea* Thüm. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *laricis-epitea* (Kleb.) Bagyanarayana

Hetereu-form, but occurrence of forms with facultative host alternation and hemi-forms probable:

0,I on: *Larix decidua*, (*L. kaempferi*)

II,III on: *Salix alpina*?, *S. arbuscula* agg., *S. aurita*?, *S. breviserrata*, *S. cinerea*, *S. daphnoides*, *S. eleagnos*, *S. glabra*, *S. helvetica*, *S. herbacea*, *S. myrsinifolia*, *S. purpurea*, *S. reticulata*, *S. retusa*, *S. serpillifolia*, *S. waldsteiniana*, (*S. bicolor*, *S. caesia*, *S.* ×*calodendron*, *S.* ×*dasyclados*, *S. foetida*, *S. fragilis*, *S. hastata*, *S. hegetschweileri*, *S. pentandra*, *S. triandra*, *S. viminalis*)

II,(III) on: *Salix caprea*?

II,(III) on: *Salix appendiculata*?, *S.* ×*smithiana*? – less susceptible hosts

Spermatogonia round to conical, subcuticular, 70–100 µm in diam., 30–40 µm high. – **Aecia** hypophyllous, single or in lines, 0.5–1.5 mm, pale orange. – **Aeciospores** globoid, ovoid or angular, 15–25 × 10–21 µm; wall 1.5–3 µm thick, finely verrucose (approx. 4 warts/µm²); warts consisting of very short cylinders of wall material; distance of warts approx. 1 µm. – **Uredinia** hypophyllous or epiphyllous, 0.25–1.5 mm, orange-yellow, in yellow spots. Paraphyses capitate or clavate, irregular, 35–80 µm long; apex 15–24 µm in diam.; wall thickness variable, 3–5 µm, up to 10 µm in the apex. – **Urediniospores** mainly broadly obovoid, occasionally ellipsoid, round or angular, 12–25 × 9–19 µm; wall usually thick (1.5–3.5 µm) but without thin areas, moderately densely echinulate (approx. 0.55 spines/µm²; see Fig. 28c, p. 216), spine distance 2–3 µm (spine distances vary between specialised forms of *M. laricis-epitea*). – **Telia** hypophyllous, very occasionally also epiphyllous, subepidermal, dark brown, small (0.25–1 mm) but in high densities or confluent at times, not very conspicuous. – **Teliospores** prismatic, rounded at both ends, 20–50 × 7–14 µm; wall brownish; wall thickness even, less than 1 µm. – References: Gäumann (1959: 152), Helfer (1992: 130).

Melampsora laricis-epitea is reported to show a number of specialised forms (Fischer 1904; Klebahn 1914; Jørstad 1953; Gäumann 1959):

- f.sp. *typica* Kleb. infects *Salix aurita*, *S. caprea*, *S. cinerea* and *S. viminalis* heavily, and *S. daphnoides*, *S.* ×*dasyclados*, *S. fragilis*, *S. purpurea* and *S.* ×*smithiana* scarcely.

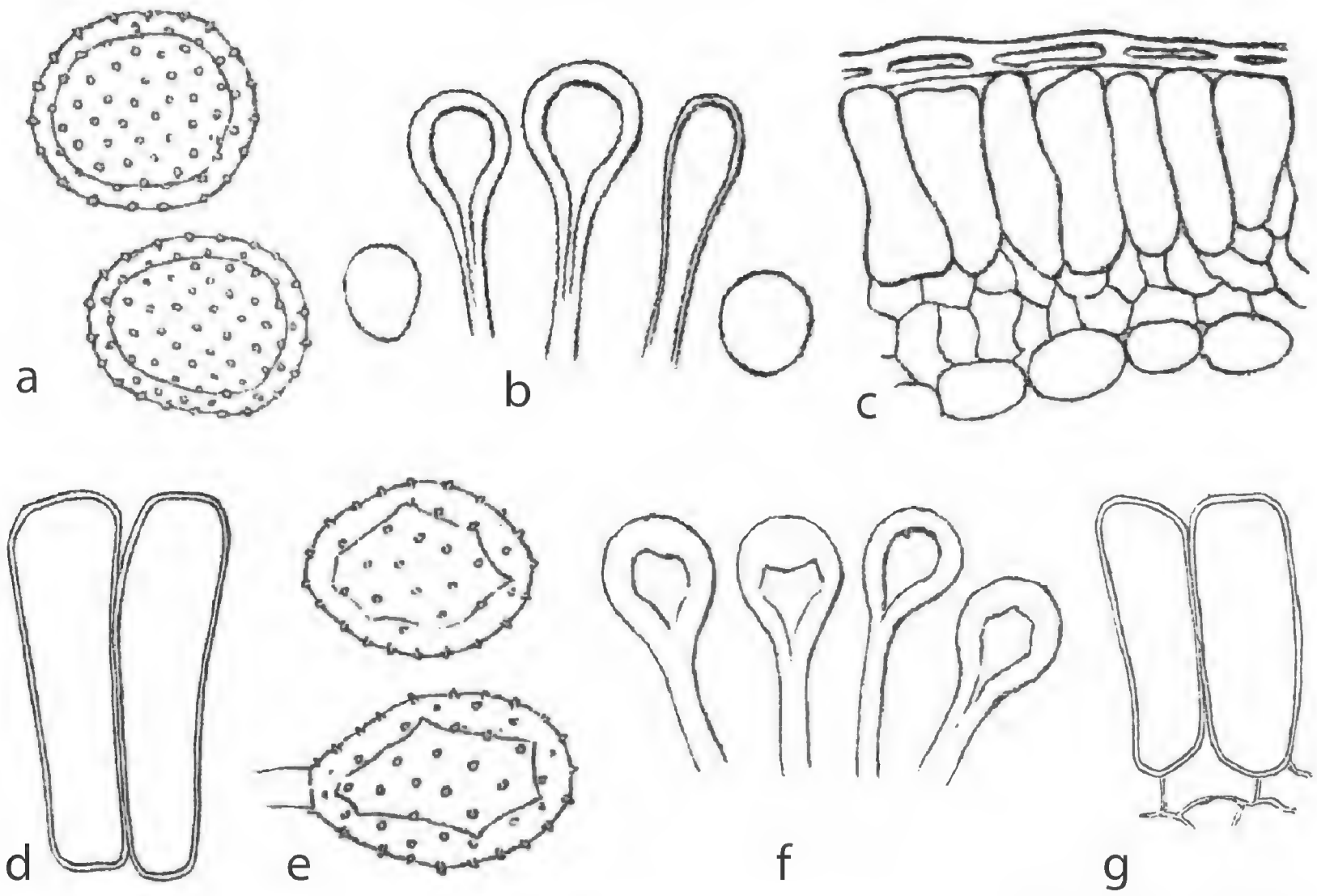


Figure 31. *Melampsora laricis-epitea*. **a–d.** f.sp. *typica* on *Salix viminalis*: **a.** Urediniospores; **b.** Paraphyses with urediniospores on the same scale; **c.** Telium in vertical section; **d.** Teliospores; **e–g.** f.sp. *laricis-daphnoidis* on *Salix daphnoides*: **e.** Urediniospores; **f.** Paraphyses; **g.** Teliospores. The specialised forms differ slightly in dimension of spores, wall thickness of spores and paraphyses, and spine density; (**a–g** from Klebahn 1914: 794).

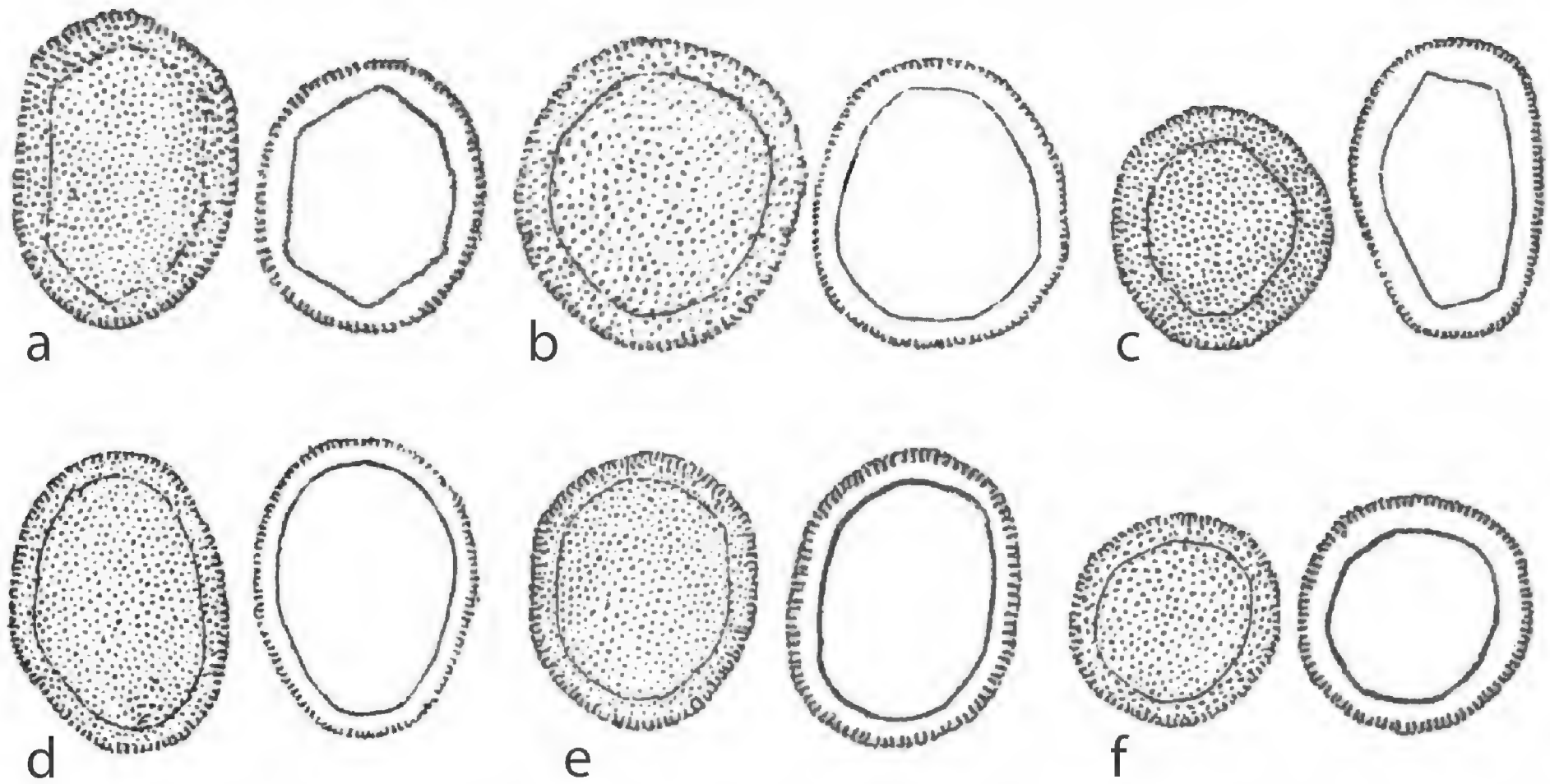


Figure 32. *Melampsora*, aeciospores on *Larix decidua* in comparison (combined view and optical section): **a.** *Melampsora farinosa*, wall sometimes thinner at certain spots; **b.** *M. laricis-epitea* f.sp. *typica*; **c.** *M. laricis-epitea* f.sp. *laricis-daphnoidis*; **d.** *M. laricis-pentandrae*; **e.** *M. laricis-populina*; **f.** *M. laricis-tremulae*; (**a–f** from Klebahn 1914: 766, 782, 794).

Figure 33. *Melampsora laricis-epitea* on *Larix decidua*: aecia on needles found in Austria (Hochschwab) in close vicinity to uredinia on *Salix glabra*. The colour of the spore mass is deep orange, and the aecia are arranged in short lines on discoloured areas of the needles (upper and lower side). For SEM photos of the aeciospores see Fig. 23 (p. 208).

- f.sp. *laricis-daphnoidis* Kleb. infects *S. daphnoides* heavily, and *Salix aurita*, *S. cinerea* and *S. viminalis* scarcely.
- f.sp. *laricis-nigricantis* Schneid.-Or. infects *S. glabra*, *S. hegetschweileri* and *S. myrsinifolia* heavily, and *S. appendiculata*, *S. arbuscula* agg., *S. cinerea*, *S. daphnoides*, *S. fragilis*, *S. herbacea*, *S. eleagnos* and *S. reticulata* scarcely.
- f.sp. *laricis-purpureae* Schneid.-Or. infects *S. aurita*, *S. daphnoides* and *S. purpurea* heavily, and *S. appendiculata*, *S. caprea*, *S. cinerea*, *S. eleagnos* and *S. myrsinifolia* scarcely.
- f.sp. *laricis-retusae* E. Fisch. infects *S. foetida*, *S. hastata*, *S. helvetica*, *S. herbacea*, *S. myrsinifolia*, *S. retusa*, *S. serpillifolia* and *S. waldsteiniana* heavily, and *S. daphnoides* and *S. reticulata* scarcely.
- f.sp. *laricis-reticulatae* Schneid.-Or. infects *S. hastata* and *S. reticulata* heavily, and *S. herbacea* scarcely.

Klebahn (1914) has demonstrated that small morphological differences between some of these forms do exist:

- f.sp. *typica* Kleb. – Aeciospores 15–21 × 10–18 µm; wall thickness 1.5 µm. – Urediniospores broadly obovoid, occasionally globoid or slightly angular, 13–25 × 9–19 µm; wall thickness 1.5–2.5 µm; spine distance 2 µm. – Telia only hypophyllous.
- f.sp. *laricis-daphnoidis* Kleb. – Aeciospores 17–21 × 12–16 µm; wall thickness 1.5–2.5 µm. – Urediniospores broadly obovoid or slightly elongate, 16–23 × 12–14 µm; wall thickness 2.5–3.5 µm; spine distance 2.5–3 µm. – Telia only hypophyllous.
- f.sp. *laricis-retusae* E. Fisch. (Fig. 28c, p. 216). – Aeciospores 18–25 × 14–21 µm; wall thickness 2–3 µm. Capitate paraphyses surround aecia. – Urediniospores 18–22 × 14–18 µm; wall thickness 2 µm; spine distance 2 µm. – Telia hypophyllous and epiphyllous.

Remarks. Wilson and Henderson (1966) stated that it is impossible to say, without inoculation experiment, to which species of *Melampsora* any given aecium on larch has to be assigned. However, Gäumann (1959) and Blumer (1963) used the colour of *Larix* aecia as a character for distinguishing *Melampsora* species in the aecial stage. According to these authors, only two species (*M. laricis-pentandrae* and *M. laricis-populina*) have bright orange aecia. The aecia of the other species (*M. laricis-epitea*, *M. farinosa*, *M. laricis-tremulae*) are

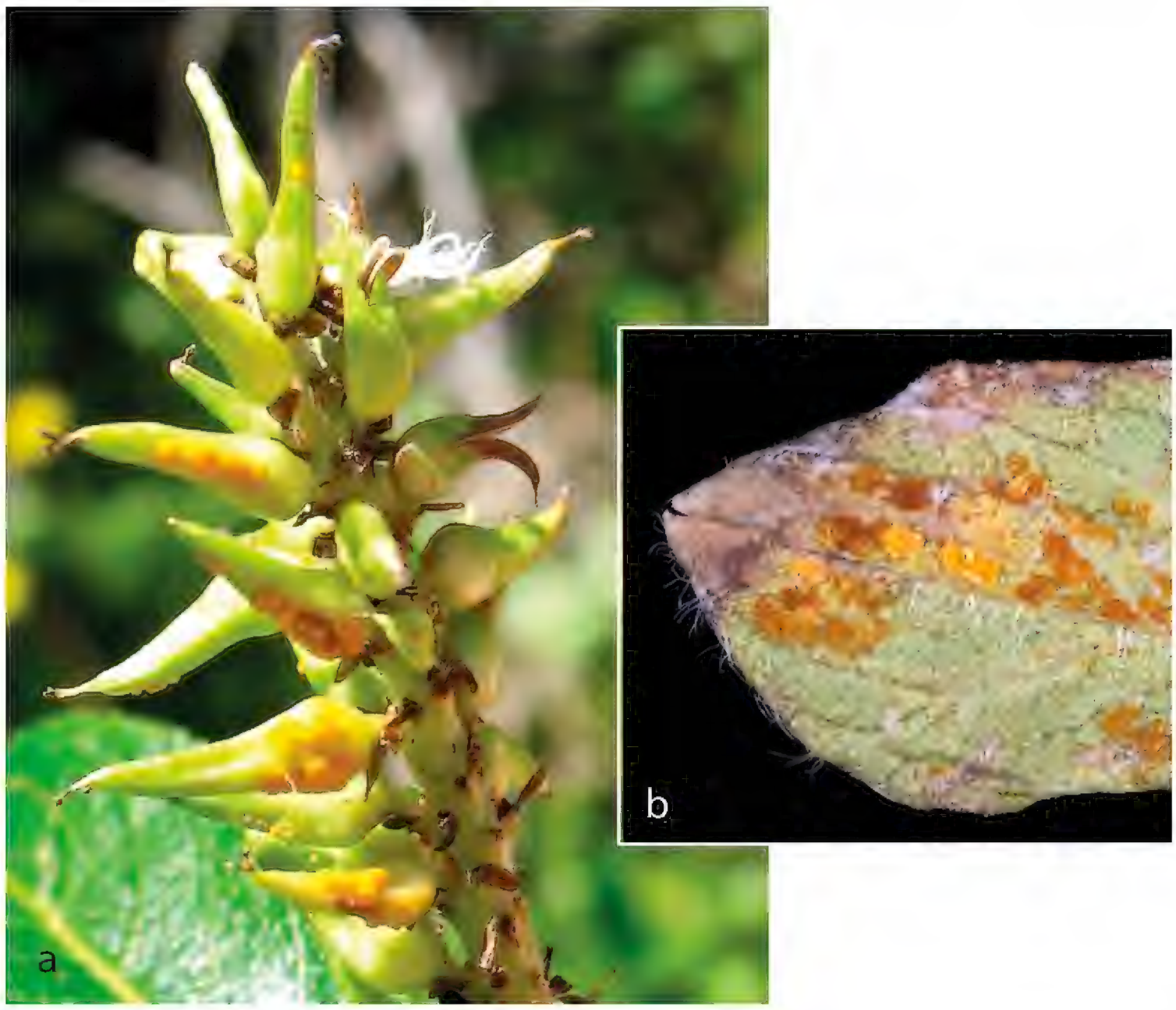


Figure 34. *Melampsora laricis-epitea*. **a.** Uredinia on fruits of *Salix glabra*; **b.** Hypophyllous uredinia and telia on *Salix retusa*.

pale orange. Moreover, collections of *M. laricis-tremulae* have smaller aeciospores (14–17 × 12–16 µm) with thinner walls (about 1 µm) than collections of *M. laricis-epitea*, *M. farinosa*, *M. laricis-pentandrae* and *M. laricis-populina*. Aeciospore dimensions and wall thickness of these four species are very similar, and do not permit safe assignment. We found aecia on larch in close vicinity to uredinia on *Salix glabra*. This is the only recent collection of aecia on larch in Austria. We assigned them to *M. laricis-epitea*. To our knowledge no evidence is provided for the occurrence of another *Melampsora* species on *S. glabra*.

In comparison with other *Melampsora* species on willow, *M. laricis-epitea* is the most widespread and most complex in its host range. In contrast to information given by Gäumann (1959), Pei (2005) and Ciszewska-Marciniak and Jedryczka (2011), Klebahn (1914) did not list *Salix caprea* as a natural host of *M. laricis-epitea*. He noted that this host-parasite combination is the result of artificial inoculation. Members of the *M. epitea* complex and *M. farinosa* clearly differ in telia morphology. Collections on *S. caprea* with single and rather large (up to 3 mm in diam.) uredinia probably belong to *M. farinosa*. Uredinia of *M. laricis-epitea* are usually smaller, but identification becomes difficult when only uredinia are present. Collections of *M. ribis-epitea* and *M. farinosa* have urediniospores with significantly lower spine density (0.3 spines/µm²) than those of *M. laricis-epitea*; collections of *M. arctica* (syn. *M. alpina*) have significantly greater spine density (0.9 spines/µm²). Collections of *M. laricis-epitea* have significantly longer and narrower urediniospores, which are less globose than in collections of *M. ribis-epitea*.

Even some specialised forms of *Melampsora laricis-epitea* differ morphologically (see above). Collections of *M. laricis-epitea* on *Salix retusa* have uredinial paraphyses with apically thicker walls (often up to 6 µm) than collections on *S. caprea* × *viminalis* (= *S.* ×*smithiana*) and *S. glabra* (up to 4–5, rarely 6 µm). One may pose the question if some of these forms do represent distinct taxa. We think that the taxonomy of the whole *M. laricis-epitea* complex needs revision.

Brandenburger (1995) assigned a Swiss collection on *Salix aurita* to *M. laricis-epitea*. His assignment is based on the following morphological characters. – Uredinia hypophyllous, 0.5 mm in diam., causing yellowish-brownish spots (1 mm in diam.) on the upper sides of the leaves. Paraphyses numerous, capitate, up to 72 µm long; head up to 22 µm wide; wall thickened up to 7 µm at the apex. – Urediniospores globoid to ovoid, 20–24 × 15–19 µm; wall up to 3.5 µm thick; distance of spines about 2 µm.

Salix alpina has not been listed as host of *Melampsora* by Gäumann (1959). The closely related *S. myrsinites* has been reported as host of *M. arctica* from N Europe. We assigned Austrian collections on *S. alpina* to *M. laricis-epitea* because of the following morphological characters. – Uredinial paraphyses ± capitate; wall thickened up to 6.5–7 µm at the apex. – Urediniospores globose to subglobose, about 17 µm in diam.; distance of spines 2–2.5 µm. – Most forms of *M. laricis-epitea* have less globose urediniospores, therefore the affiliation of this rust remains uncertain.

Uredinia and telia on *Salix breviserrata* have been found in the Styrian Alps by Riegler-Hager (unpublished data). *S. alpina* and *S. breviserrata* are members of the *S. myrsinites* agg.

Uredinia and telia on *Salix caesia* have been found in the French Alps. Mayor (1969) assigned them to *M. laricis-epitea*, based on the following morphological characters. – Uredinia on both sides of the leaves but mostly hypophyllous, 0.5 mm in diam. Paraphyses numerous, capitate, 57 µm long; head 14–21 µm wide; wall thickened up to 6 µm at the apex. – Urediniospores globoid to subgloboid or obovoid, 15–19 × 12–19 µm; wall 2–2.5 µm thick. – Telia hypophyllous, brown then black. – Teliospores prismatic, rounded at both ends, 21–42 × 9–14 µm, brown; wall thickness even (1–1.5 µm). – It still has to be proven if *M. laricis-epitea* can infect *Salix caesia*. No successful inoculation experiments have been reported so far.

Salix caprea and *S. cinerea* are listed as hosts of *Melampsora farinosa*, *M. abietis-caprearum*, *M. euonymi-caprearum*, *M. laricis-epitea* and *M. ribis-epitea* by Gäumann (1959), but Hylander et al. (1953) and Pei (2005) emphasised that *S. cinerea* is probably no natural host of *M. farinosa*. This host-parasite combination is based on an inoculation experiment. However, Henderson (2004) reported *S. cinerea* as host of *M. farinosa* and *M. epitea* s.l. from the British Isles, but he listed only *S. caprea* as host of *M. farinosa*. The host-parasite combination *S. caprea-M. laricis-epitea* has been recorded by several authors. The records require confirmation (see Klebahn 1914). In Austria, telia of *M. laricis-epitea* have not been found on *S. caprea* (Zwetko 2000).

Salix glabra and *S. retusa* are rather frequently attacked hosts of *M. laricis-epitea* in Austria.

Pei and Ruiz (2000) used amplified fragment length polymorphism (AFLP) to examine genetic variation in *Melampsora* on *Salix viminalis*, the most important willow species for renewable energy in the UK. They started from two forms, of which one infects young leaves, shoot tips and young stems, and causes stem cankers. It overwinters in buds or stems of infected willows. No telia have been found in nature. Within this stem infecting form, AFLP patterns were very similar, indicating that this form is an asexual population and may have a clonal lineage. The taxonomic status of the stem infecting form is not yet certain. The second form infects only leaves and overwinters as teliospores on fallen willow leaves. It alternates on *Larix decidua* and completes a full sexual life-cycle. Pei and Ruiz (2000) assigned it to *M. epitea* f.sp. *laricis-epitea typica*. AFLP profiles varied between most of the isolates within the leaf infecting form. Pei and Ruiz (2000) supposed that the stem infecting form may have evolved from a leaf infecting form by gradually shifting its niche from fully expanded leaves to very young leaves and shoots. – Klebahn (1914) reported that *S. viminalis* is a very common host of *M. laricis-epitea* f.sp. *typica* in Brandenburg (Germany). Mayor (1972) recorded this willow species as host of *M. laricis-epitea* from Switzerland. Ciszewska-Marciniak et al. (2010) stated that *M. laricis-epitea* f.sp. *typica* is a dominant pathogen of *S. viminalis* in Poland. Hence, this common rust is expected to occur also in Austria on *S. viminalis*.

For the distribution of *Melampsora laricis-epitea* in Austria see Poelt and Zwetko (1997: 79).

11 *Melampsora repentis* Plowr.

Figs 35, 36

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. arctica* Rostr. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *repentis* (Plowr.) Boerema & Verh.; *M. orchidis-repentis* Kleb.

Hetereu-form:

0,I on: *Dactylorhiza majalis*, *Neotinea ustulata* [syn. *Orchis u.*], *Ophrys sphegodes*, *Orchis mascula*, (*Anacamptis morio* [syn. *Orchis m.*], *Dactylorhiza incarnata*, *D. maculata*, *D. sambucina*, *D. traunsteineri*, *Epipactis helleborine*, *Gymnadenia conopsea*, *Neottia ovata* [syn. *Listera o.*], *Ophrys insectifera*, *Orchis militaris*, *O. purpurea*, *Platanthera bifolia*, *P. chlorantha*, *Pseudorchis albida*)

II,III on: *Salix repens*, (*S. aurita*, *S. caprea*?, *S. eleagnos*?, *S. purpurea*?, *S. repens* subsp. *rosmarinifolia*, *S.* ×*stipularis*?)

Spermatogonia subepidermal, often underneath stomata, 170 µm wide, 80 µm high. – **Aecia** hypophyllous in discoloured spots, bright orange, in groups or in circular arrangement, sometimes confluent and then up to 20 mm long, single sori 1–2 mm in diam. – **Aeciospores** angular-globoid, 15–20 × 11–15 µm; wall 1–1.5 µm thick, very finely verrucose (>4 warts/µm²); distance of warts less than 1 µm. – **Uredinia** hypophyllous and crowded on fruits, very small (0.25–0.5 mm in diam.), dark orange, producing yellow spots on upper side of the leaf. Paraphyses distinctly capitate, 40–70 µm long; head 16–20 µm wide; stem thin (3–5 µm); head nearly globoid or subgloboid; wall of the head 2–4(–5) µm thick. – **Urediniospores** globoid or ovoid, 13–17 × 12–14 µm; wall 1–1.5 µm thick, ± densely echinulate; distance of warts 1.5 µm (after Klebahn 1914 and Gäumann 1959). – Our examinations of one collection on *S. repens* from Austria (Carinthia, Gailtaler Alpen, Farchtner See) and of two collections from Finland (Mycotheca fennica, nos 648, 649) show rather similar morphological characters, but the spine distances are different. In the Finnish collections the distance is 1.5 µm, in the Austrian ones it is (1.5–)2–2.5 µm. The spine density counted in the Austrian collection is in accordance with that of *M. repentis* reported by Helfer (1992: 123) who counted 0.50 spines/µm². – **Telia** hypophyllous, subepidermal, small (0.5 mm). – **Teliospores** prismatic, rounded at both ends, 16–48 × 7–14 µm; wall thickness even, 1 µm. – References: Klebahn (1914: 802–803), Gäumann (1959: 162–163), Helfer (1992: 131).

Remarks. Morphologically, this rust resembles *Melampsora laricis-epitea* (Klebahn 1900; Gäumann 1959), which does not occur on *Salix repens*. According to Gäumann (1959), only two *Melampsora* species, *M. abietis-caprearum*

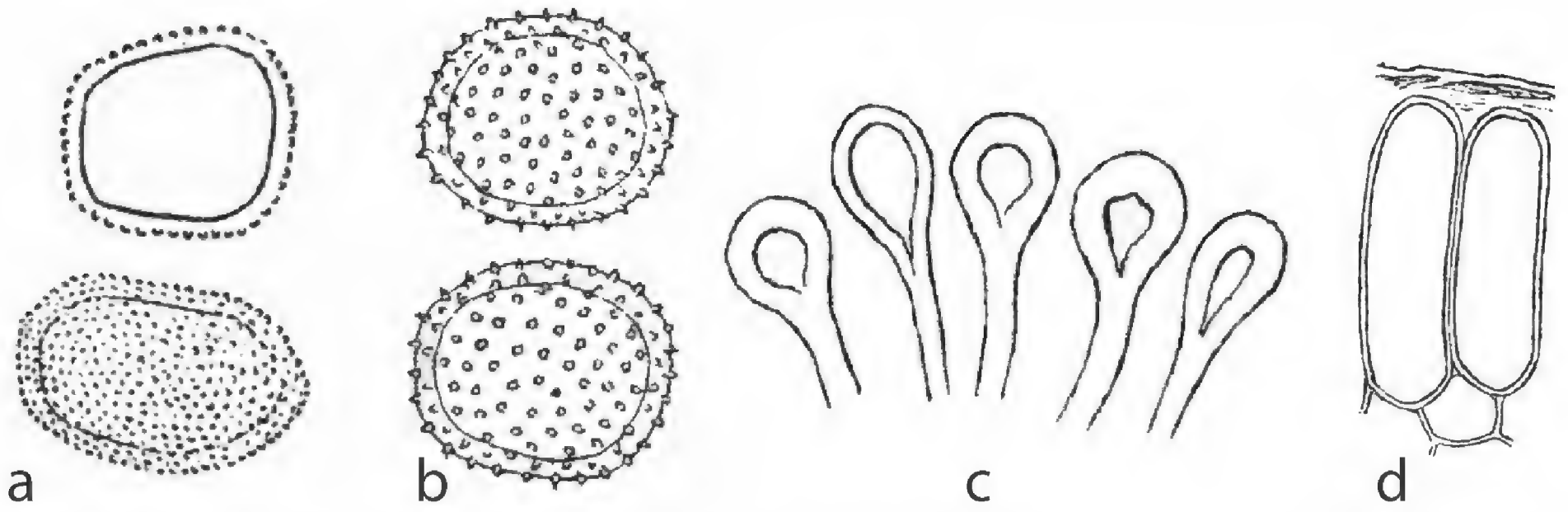


Figure 35. *Melampsora repentis*. **a.** On *Dactylorhiza majalis*: aeciospores; **b–d.** On *Salix repens*: **b.** Densely echinulate urediniospores; **c.** Paraphyses; **d.** Teliospores; (**a–d** from Klebahn 1914: 812, as *M. orchidi-repentis*).

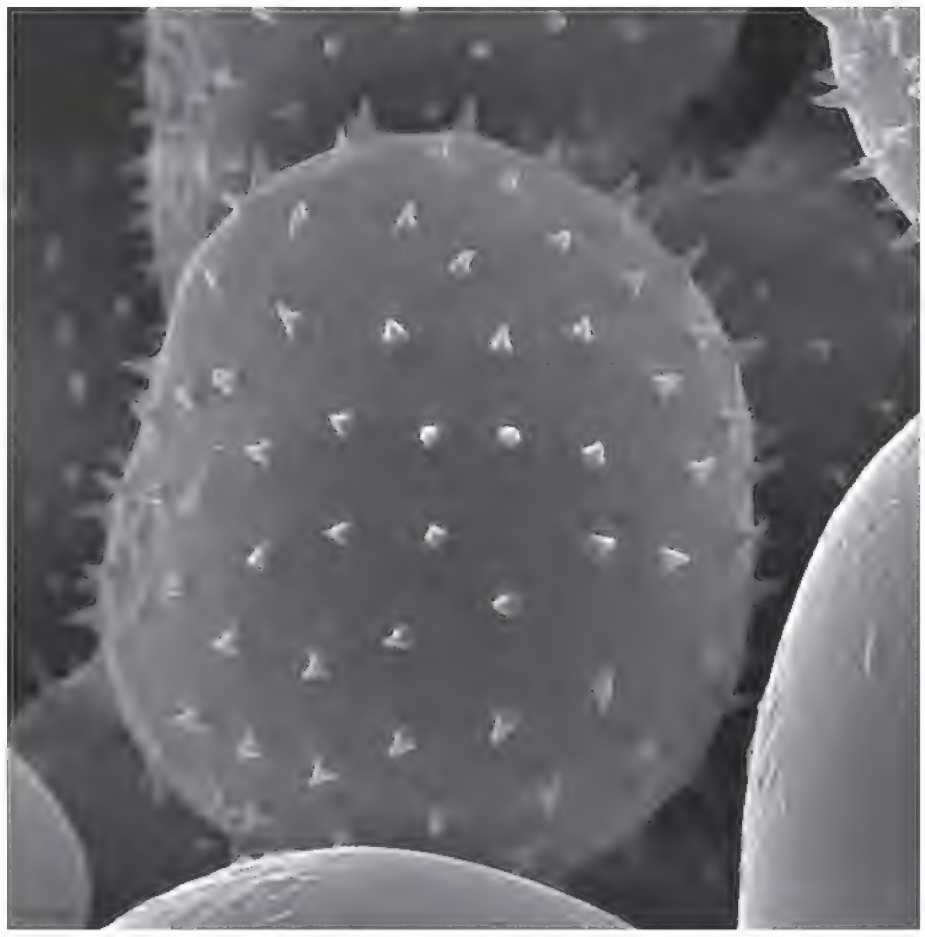


Figure 36. *Melampsora repentis* on *Salix repens*: urediniospore with less densely echinulate wall ornamentation in SEM; specimen collected in Austria (photo by Paul Blanz).

and *M. repentis* infect *S. repens*. Gäumann noted that *M. repentis* differs from *M. abietis-caprearum* in its less densely echinulate urediniospores. We suppose that this character does not permit a safe determination. Uredinial paraphyses show better differential characters (distinctly capitate in *M. repentis*, ± clavate in *M. abietis-caprearum*). – Helfer (1992) used differences in urediniospore spine density to help to characterise willow rusts, but urediniospore spine distances in *M. abietis-caprearum* and *M. repentis* reported by Gäumann (1959) are not in accordance with spine densities measured by Helfer (1992). While Gäumann reported 1 µm distance for *M. abietis-caprearum*, 1.5 µm for *M. repentis* and 2 µm for *M. laricis-epitea*, Helfer counted 0.6 spines/µm² in *M. abietis-caprearum*, 0.55 in *M. laricis-epitea* and 0.50 in *M. repentis*.

Poelt and Zwetko (1997: 82) reported only two finds of *Melampsora repentis* on *Salix repens* from Austria. One report is based on old literature (Magnus 1905), one on herbarium material (GZU). We examined the Austrian collection and two collections from Finland. The Austrian collection differs from the Finnish collections in spine distance and slightly in wall thickness (scarcely 1 µm in the Finnish collections, 1.5 µm in the Austrian one). Therefore, we suppose that *M. repentis* includes morphologically different forms. It remains unknown if these forms also differ in their host range. *Melampsora repentis* is reported from various aecial hosts, but its telial host range is rather narrow.

In Switzerland, Mayor (1924) found aecia on *Anacamptis morio* (syn. *Orchis m.*) in close vicinity to *Salix caprea*, *S. eleagnos* and *S. purpurea*, but in the absence of *S. repens* and *S. aurita*. Therefore, he supposed that the three former willow species may serve as telial hosts of *Melampsora repentis*. Gäumann (1959) noted that only the host-parasite combinations *Salix repens-M. repentis* and *Salix aurita-M. repentis* have been proven experimentally. – Braun (1982) reported *S. repens* subsp. *rosmarinifolia* and *S.* ×*stipularis* as hosts of *M. arctica* from Germany. Majewski (1977) reported *S. repens* subsp. *rosmarinifolia* as hosts of *M. repentis* from Poland, Roivainen (Mycotheca fennica, no 649) from Finland. – *Salix repens* has been reported as host of *M. farinosa* from Germany (Brandenburger 1994). To our knowledge this report is based on old literature (Klebahn 1890b). However, herbarium specimens of *M. farinosa* on *S. repens* were not available. – In Great Britain *M. repentis* is uncommon but may persist in the buds of willows and therefore can occur without orchids being present (Helfer 1992).

12 *Melampsora reticulatae* A. Blytt

Fig. 37

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *reticulatae* (A. Blytt) Jørst.; *M. epitea* Thüm. f.sp. *reticulatae* (A. Blytt) Jørst.

Hetereu-form:

0,I on: *Saxifraga aizoides*, *S. moschata*, (*S. exarata*, *S. muscoides*)

II,III on: *Salix reticulata*, (*S. hastata* and its hybrids, *S. myrtilloides*, *S. retusa*)

Figure 37. *Melampsora reticulatae* on *Salix reticulata*: uredinia (photo by Julia Kruse).

Spermatogonia epiphyllous, single or in groups, 150 µm in diam., 90–125 µm high. – **Aecia** epiphyllous or amphigenous, single or a few dispersed on the leaves, 0.5–1 mm in diam., yellow-orange; semi-systemic infection, affected leaves can be identified by their yellow discolouration. – **Aeciospores** globoid, ovoid or slightly angular, 16–25 × 14–20 µm (after Gäumann 1959 and Helfer 1992), (20–)22–26(–32) × (14–)18–22(–25) µm, mean 23.2–24.0 × 19.3–21.0 µm (after Brandenburger 1997b); wall thickness 2–4 µm, densely verrucose (approx. 4 warts/µm²); distance of warts less than 1 µm. – **Uredinia** hypophyllous, scattered or in groups, roundish, 0.5–1 mm, bright yellow-orange. Paraphyses numerous, capitate, 60–95 µm long, head 18–41 µm wide (after Gäumann 1959 and Helfer 1992), 25–35 µm wide (after Wilson and Henderson 1966); wall thickness up to 10 µm. – **Urediniospores** globoid, ellipsoid or pear-shaped, very varied in shape and size, 17–35 × 15–23 µm (after Gäumann 1959 and Helfer 1992), 24–32 × 16–22.5 µm (after Wilson and Henderson 1966), (21–)22–26(–31) × (18–)20–23(–25) µm, mean 24.0 × 21.3 µm (after Brandenburger 1997b); wall 2–3.5 µm thick, evenly echinulate (0.45 spines/µm²). – **Telia** mainly epiphyllous (hypophyllous after Brandenburger 1997b), subepidermal, small (0.3–0.5 mm in diam.), reddish-brown, occasionally filling the spaces between leaf veins completely. – **Teliospores** prismatic, rounded at both ends, 35–44 × 10–13 µm; wall thickness even, 1 µm. – References: Gäumann (1959: 172–173), Helfer (1992: 131), Brandenburger (1997b: 73).

Remarks. Gäumann (1959) noted that only the host alternation *Saxifraga aizoides-Salix reticulata* has been proven experimentally. Nevertheless, Brandenburger (1994) assigned aecia found on *Saxifraga moschata* and *S. muscoides* in Germany to *Melampsora reticulatae* as well. Brandenburger (1997b) reported *M. reticulatae* on *Saxifraga aizoides*, *Saxifraga moschata* and *Salix reticulata* also from Graubünden (Switzerland). In one collection on *Saxifraga moschata*, Brandenburger (1997b) found smaller and more globoid aeciospores than usually in collections on *Saxifraga aizoides* and *S. moschata*. In this collection the spores are (16–)18–21(–23) µm long and (14–)17–20(–22) µm wide (mean 19.8 × 18.1 µm). Urban and Marková (2009) reported aecia of *M. reticulatae* on *Saxifraga aizoides* and *S. moschata* from Slovakia, Maire (1907) on *S. moschata* from the Pyrenees. Also in the Austrian Alps, aecia on *Saxifraga moschata* have been collected in close vicinity to *Salix reticulata* many times (Poelt and Zwetko 1997). Therefore, they have been assigned to *M. reticulatae*. *Saxifraga moschata* has been reported by Mayor (1970) as aecial host of *M. alpina* (= *M. arctica*) as well, on the basis of material collected in the Pyrenees.

The telial host, *Salix reticulata* is parasitised by two *Melampsora* species, *M. reticulatae* and *M. laricis-epitea*, which is confirmed by inoculation experiments. Both are members of the *M. epitea* species complex. Jørstad (1940) and Wilson and Henderson (1966) recognised two varieties within *M. epitea* s.l.; *M. epitea* var. *reticulatae* (= *M. reticulatae*) differs from var. *epitea* (incl. *M. arctica*, *M. laricis-epitea* and other species) in its larger urediniospores (24–32 × 16–22.5 µm) and larger uredinial paraphyses (up to 90 µm long, with 25–35 µm wide head and up to 10 µm thick wall). In contrast, the urediniospores of *M. laricis-epitea* are 12–25 µm long and 9–19 µm wide, the paraphyses up to 80 µm long, with 15–24 µm wide head and 3–5 µm thick wall (sometimes up to 10 µm in the apex).

Henderson (1953) has used cross-inoculations to investigate the relation between rust morphology and host specificity. He showed that *Melampsora epitea* var. *epitea* (in this case: *M. arctica*) alternates between *Salix herbacea* and *Saxifraga hypnoides* and that *M. epitea* var. *reticulatae* (*M. reticulatae*) alternates between *Salix reticulata* and *Saxifraga aizoides*. Urediniospores found on *Salix herbacea* were used to inoculate *Salix herbacea*, *S. lanata*, *S. repens*, *S. reticulata* and *S.* ×*sadleri*. Only *Salix herbacea* became infected. From the same Scottish locality urediniospores on *Salix reticulata* were used to inoculate *Salix herbacea*, *S. lanata*, *S. repens*, *S. reticulata* and *S.* ×*sadleri*. Only *Salix reticulata* became infected. The results from the inoculation experiments show that the rusts on *Salix herbacea* and *S. reticulata* are strictly specialised. However, Jørstad (1951) supposed that *Salix herbacea* may serve as host for *M. epitea* var. *reticulatae* in Iceland. Gjærum (1974) also reported this host-parasite combination from Iceland, but not from the Continent (Scandinavia).

Salix retusa has been reported as host of *Melampsora reticulatae* from Germany (Brandenburger 1994), while Gäumann (1959) stated that inoculation experiments with this host plant show negative results. The report of Brandenburger is based on old literature (Huber and Poeverlein 1954). The same authors recorded *Salix retusa* as host for another rust, *M. arctica*. This rust typically infects *Salix herbacea*.

Jørstad (1940) emphasised that *Melampsora epitea* var. *reticulatae* is the only rust found in N Norway on *Salix myrtilloides*. Jørstad (1940, 1953) reported that aecia on *Saxifraga aizoides* correspond to *M. epitea* var. *reticulatae* on *Salix reticulata*, very probably also on

Salix hastata and hybrids. Jørstad (1953) and Gjærum (1974) have also assigned Scandinavian collections on *Salix glauca*, *S. glauca* var. *appendiculata*, *S. hastata*, *S. herbacea* × *lapponum* and *S. myrtilloides* to *M. epitea* var. *reticulatae*. Hence, *Salix glaucosericea* (a member of the *S. glauca* group) may serve as host in the Alps.

Melampsora reticulatae can persist on its aecial and uredinial hosts (Henderson 1953; Gäumann 1959). – For records of *M. reticulatae* in Austria see Poelt and Zwetko (1997: 82).

13 *Melampsora ribis-epitea* Kleb.

Fig. 38

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. epitea* Thüm. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *ribis-purpureae* (Kleb.) Bagyanarayana (as *ribesii-purpureae*)

Hetereu-form:

(0,I on: *Ribes alpinum*, *R. aureum*, *R. nigrum*, *R. rubrum*, *R. sanguineum*, *R. uva-crispa*, *R. uva-crispa* subsp. *grossularia*)

II,(III) on: *Salix appendiculata*, *S. aurita*?, *S. myrsinifolia*, (*S. arbuscula* agg., *S. caprea*, *S. cinerea*, *S. eleagnos*, *S. foetida*, *S. viminalis*?)

Spermatogonia conical to cushion shaped, 150 µm in diam., 60 µm high. – **Aecia** hypophyllous, single or in groups, often confluent, 0.5–1.5 mm, orange. – **Aeciospores** mainly globoid, rarely angular or elongated, 17–24 × 15–20 µm; wall thickness up to 3 µm with thin areas, densely and finely verrucose (approx. 4 warts/µm²); distance of warts 1 µm or less. – **Uredinia** hypophyllous, medium-sized (0.5–1 mm), forming round cushions, single or scattered, producing bright yellow spots on the upper side of the leaves. Paraphyses capitate to clavate, head often tapering towards the stem, 55–70(–75) µm long, head 16–24 µm wide, stem 4–7 µm; wall thickness even, 2.5–4 µm (rarely 5 µm). – **Urediniospores** mainly globoid, rarely slightly angular, 16–20 × 14–18 µm (after Gäumann 1959 and Helfer 1992), (14–)16–20(–23) × (13–)14–17(–20) µm, mean 18.0–19.3 × 15.1–16.6 µm (after Brandenburger 1995, 1996); wall thickness 3–3.5 µm, with thin areas, distantly echinulate. – The spine distance (2 µm) reported by Gäumann (1959) and Brandenburger (1996) and the spine density (0.3 spines/µm²) measured by Helfer (1992) show discrepancies. We observed (2–)2.5–3 µm spine distance in the Austrian collections, in accordance with the measurements of Helfer (l.c.). – **Telia** hypophyllous, subepidermal, single or in groups, occasionally densely covering larger areas, individually small (0.5 mm), brown. – **Teliospores** irregular, prismatic, rounded at both ends, 20–30 × 7–11 µm; wall thickness even, 1 µm. – References: Gäumann (1959: 168–169), Helfer (1992: 132), Brandenburger (1995: 134, 1996: 13).

Melampsora ribis-epitea is reported to show two specialised forms (Mayor 1958; Gäumann 1959):

- f.sp. *ribis-auritae* Kleb. on several *Ribes* species and *Salix aurita*; *S. caprea* and *S. cinerea* are less susceptible hosts.
- f.sp. *ribis-grandifoliae* Schneid.-Or. on *Ribes alpinum* and *Salix appendiculata* and *S. aurita*; '*S. arbuscula*' is a less susceptible host.

Remarks. Brandenburger (1996) has assigned collections on *Salix appendiculata*, *S. eleagnos* and *S. myrsinifolia* from Switzerland to *Melampsora ribis-epitea*. Neither *S. eleagnos* nor *S. myrsinifolia* are listed as hosts of *M. ribis-epitea* by Gäumann (1959). The assignment is based on the following morphological characters: Uredinia hypophyllous. Paraphyses capitate, up to 75 µm long, head 18–22 µm wide, stem 5–7 µm; wall 3–4(–5) µm thick. – Urediniospores subglobose, (14–)17–21(–23) × (13–)14–17(–18) µm (mean 18.0–19.3 × 15.1–16.0 µm); wall about 3.5 µm thick. – *Melampsora abietis-caprearum* also infects *Salix appendiculata*; this rust species differs from *M. ribis-epitea* by its urediniospore shape, size and wall thickness.

Brandenburger (1997a) has reported another *Salix* species, *S. foetida* (*S. arbuscula* agg.) as host of *M. ribis-epitea* from Switzerland. His assignment is based on the following morphological characters: Uredinia hypophyllous, also on fruits. – Urediniospores subglobose, (16–)18–21(–23) × (13–)15–18(–20) µm (mean 19.2–19.5 × 16.5–16.7 µm). – Gäumann (1959) has recorded this willow species only as host of *M. laricis-epitea*. Urediniospores of *M. laricis-epitea* are slightly longer and narrower (i.e., less globose) than those of *M. ribis-epitea*.

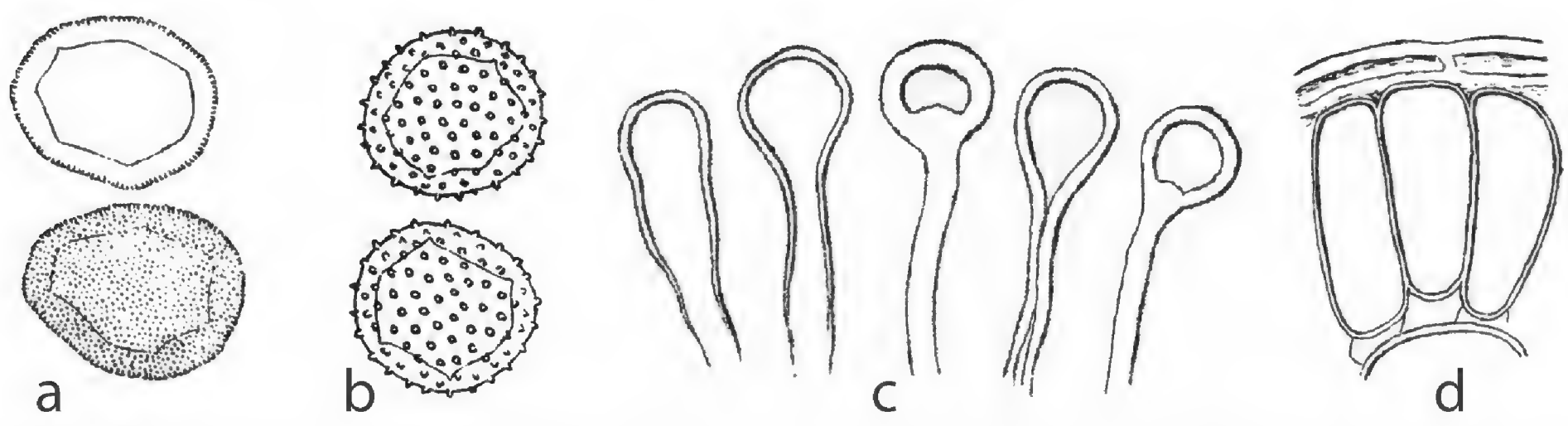


Figure 38. *Melampsora ribis-epitea*. **a.** On *Ribes nigrum*: aeciospores; **b–d.** On *Salix aurita*: **b.** Urediniospores, walls thick with thinner areas; **c.** Paraphyses; **d.** Teliospores; (**a–d** from Klebahn 1914: 794).

Salix myrsinifolia and *S. viminalis* have been reported as hosts of *Melampsora ribis-purpureae* from Norway (Jørstad 1953) and Poland (Majewski 1977); both authors did not distinguish between *M. ribis-purpureae* and *M. ribis-epitea*. Therefore, the host-parasite combination *S. viminalis-M. ribis-epitea* remains uncertain.

Poelt and Zwetko (1997: 83) did not record collections of *M. ribis-epitea* from Austria, but this rust has been found since then in Carinthia (Karawanken, Tscheppaschlucht, on *Salix appendiculata*) and in Styria (Hochschwab, am Fuß der Aflenzer Staritzen, on *S. myrsinifolia*). Also, an old report on *S. aurita* may belong to this rust species.

14 *Melampsora ribis-purpureae* Kleb.

Fig. 39

Syn. *Melampsora epitea* s.l.; *M. epitea* Thüm. var. *epitea*; *M. epitea* Thüm. emend. U. Braun (1981); *M. epitea* Thüm. f.sp. *ribis-purpureae* (Kleb.) Bagyanarayana (as *ribesii-purpureae*)

Hetereu-form:

0,I on: *Ribes alpinum*, *R. uva-crispa* agg., (*R. aureum*, *R. nigrum*, *R. rubrum*, *R. sanguineum*, *R. spicatum*, *R. uva-crispa*, *R. uva-crispa* subsp. *grossularia*)

II,III on: *Salix purpurea*, (*S. myrsinifolia*?, *S. purpurea* × *viminalis*, *S. viminalis*?)

(II,[III] on: *Salix daphnoides*) – less susceptible host

Spermatogonia protruding a little, 180 µm in diam., 60–70 µm high. – **Aecia** mainly hypophyllous, in pale yellow spots (0.5–1.5 mm), single or in often circular groups, often confluent, orange. – **Aeciospores** round, often angular, (15–)18–20(–23) × (12–)15–18(–19) µm; wall thickness 3 µm with thin areas, densely verrucose (approx. 4 warts/µm²); distance of warts less than 1 µm. – **Uredinia** mainly hypophyllous, occasionally epiphyllous, orange red, the first quite large (1.5 mm), in bright yellow spots. Paraphyses 44–70 µm long, variable in shape, capitate with 15–21 µm wide head or clavate and 12–15 µm wide above; wall thickness even, 1.5–3 µm. – **Urediniospores** mainly roundish, rarely angular, 15–23 × 14–19 µm (after Gäumann 1959 and Helfer 1992), (14–)16–19(–22) × (13–)13–16(–18) µm, mean 17.1 × 14.8 µm (after Brandenburger 1997a); wall thickness 2.5 µm, with thin areas, densely echinulate (0.6 spines/µm²); distance of spines 2–2.5 µm. – **Telia** mainly hypophyllous, occasionally epiphyllous, subepidermal, small (0.25–0.5 mm), blackish-brown, single or in groups, often covering the whole surface. – **Teliospores** irregularly prismatic, rounded at both ends, 25–35 × 7–10 µm; wall thickness even, 1 µm. – References: Gäumann (1959: 167–168), Helfer (1992: 132), Brandenburger (1997a: 47).

Remarks. *Salix purpurea* × *viminalis* has been reported as host of *Melampsora ribis-purpureae* for example from Germany (Brandenburger 1994: 26). Majewski (1977) also listed *S. viminalis* as host, but he did not distinguish between *M. ribis-purpureae* and *M. ribis-epitea*. Therefore, the host-parasite combination *S. viminalis-M. ribis-purpureae* remains uncertain. *Melampsora ribis-epitea* differs from its close relative *M. ribis-purpureae* by its thicker urediniospore walls and different *Salix* hosts.

Salix myrsinifolia and its hybrid with *S. phylicifolia* have been reported as host of *M. ribis-purpureae* from Norway by Jørstad (1953, 1964b), but he did not distinguish between *M. ribis-purpureae* and *M. ribis-epitea* either. Therefore, the host-parasite combination *S. myrsinifolia-M. ribis-purpureae* remains uncertain as well. Gäumann (1959) listed *S. myrsinifolia* as host of only two *Melampsora* species, *M. abietis-caprearum* and *M. laricis-epitea*.

Melampsora ribis-purpureae can persist on twigs of its uredinial host (Gäumann 1959). – For records of *M. ribis-purpureae* in Austria see Poelt and Zwetko (1997: 83).

15–20 *Melampsora euphorbiae* s.l. (*M. euphorbiae* complex)

15 *Melampsora euphorbiae* s.l.

= *Melampsora euphorbiae* (C. Schub.) Castagne s. Wilson and Henderson (1966)

N.B.: *Melampsora euphorbiae* s.l. and *M. euphorbiae* s. Gäumann (1959, see below) are convenient entities for the present treatment and retained here. According to the

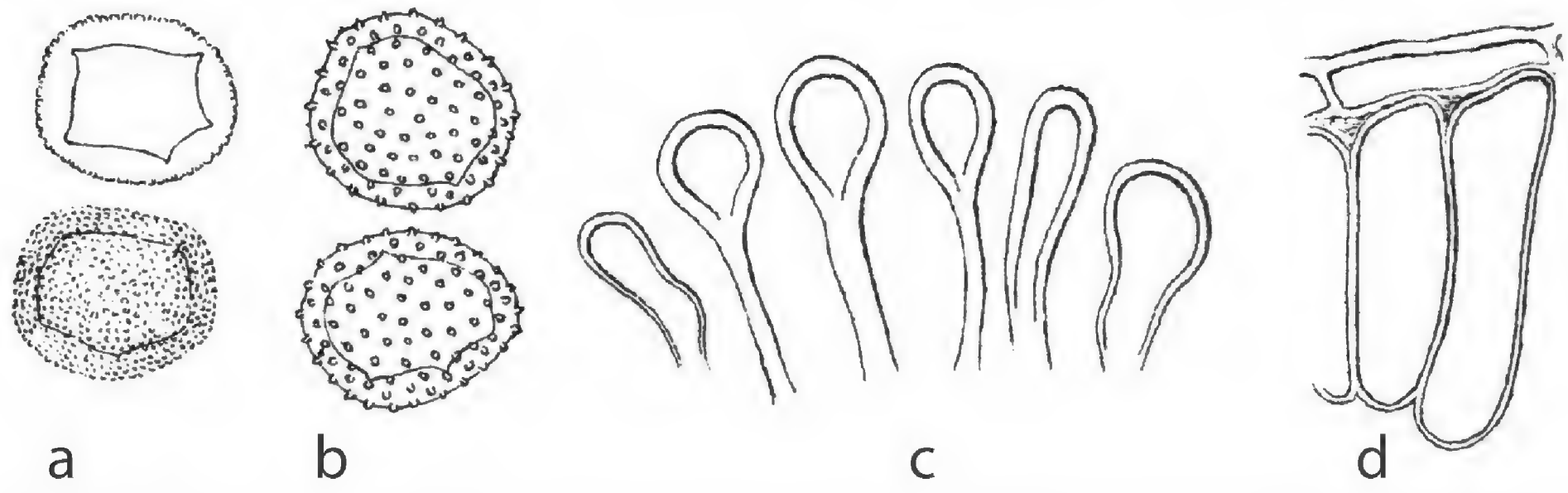


Figure 39. *Melampsora ribis-purpureae*. **a.** On *Ribes uva-crispa*: aeciospores (distinctly smaller than those of *M. ribis-epitea*); **b–d.** On *Salix purpurea*: **b.** Urediniospores; **c.** Paraphyses; **d.** Teliospores; (**a–d** from Klebahn 1914: 794).

current entry in MycoBank (2024), however, *M. euphorbiae* is now a synonym of *M. euphorbiae-helioscopiae*, with regard to the oldest epithet available in this complex.

Accepted species within the complex: ***M. euphorbiae* s. Gäumann**, ***M. euphorbiae-dulcis***, ***M. euphorbiae-gerardianae***, ***M. euphorbiae-helioscopiae***, ***M. gelmii***

Auteu-forms and forms with reduced life cycle:

0–III on: *Euphorbia angulata*, *E. cyparissias*, *E. dulcis*, *E. esula*, *E. exigua*, *E. helioscopia*, *E. lathyris*, *E. palustris*, *E. peplus*, *E. verrucosa*, (*E. carniolica*, *E. glareosa*, *E. lucida*, *E. platyphyllos*, *E. epithymoides* [syn. *E. polychroma*], *E. salicifolia*, *E. stricta*, *E. illirica* [syn. *E. villosa*], *E. virgata*?)

II,III on: *Euphorbia falcata*, (*E. seguieriana*)

The following records cannot be assigned to any species in the *M. euphorbiae* complex with certainty:

(0,I),II,III on: *Euphorbia illirica* [syn. *E. austriaca*], *E. virgata*

(0,I),II,(III?) on: *Euphorbia amygdaloides* (*M. euphorbiae-amygdaloidis* W. Muell.)

(II,III on: *Euphorbia pulcherrima*)

II on: *Euphorbia saxatilis*

The species complex is characterised by subepidermal teliospores. The urediniospores are globoid or ovoid with uniformly echinulate walls. After morphological investigations of rusts on 29 *Euphorbia* species and carrying out a number of inoculation experiments, Müller (1907) distinguished nine 'biological species': *Melampsora euphorbiae-amygdaloidis*, *M. euphorbiae-cyparissiae*, *M. euphorbiae-dulcis*, *M. euphorbiae-exiguae*, *M. euphorbiae-gerardianae*, *M. euphorbiae-pepli*, *M. euphorbiae-strictae*, *M. gelmii*, and *M. helioscopiae* s.str. However, Müller (1907) was not able to establish strictly defined morphological species and created five collective types, which include forms with morphologically similar teliospores. Since then, many authors have treated these types as provisional species (e.g., Sydow and Sydow 1915; Gäumann 1959; Brandenburger 1994; Poelt and Zwetko 1997). The morphology of urediniospores has not been studied satisfactorily. For instance, we found distinctly larger urediniospores in collections on *Euphorbia saxatilis* than in collections on *E. austriaca* and *E. virgata*. This is one of many examples for the fact that the taxonomy of rusts affecting wild plants still receives little attention, resulting in a patchy knowledge of their systematic relationship (Helfer et al. 2011).

Melampsora euphorbiae-amygdaloidis* W. Muell. on *Euphorbia amygdaloides. – Spermatogonia and aecia reported from Switzerland (Mayor 1958). – Uredinia hypophyllous, scattered or in groups, surrounded by the ruptured epidermis, yellow, about 1 mm in diam. Paraphyses capitate (to clavate); head up to 21–25(–27) µm wide; wall up to 5–6.5 µm thick. – Urediniospores globoid to ellipsoid, 21–24 × 16–21 µm; wall hyaline, (1.5–)2 µm thick, finely and densely echinulate; distance of spines about 1.5 µm (these measurements of urediniospores and paraphyses are based on Austrian collections). – Teliospores 50–90 × 8–12 µm (after Brandenburger 1985: 338; unfortunately, he did not mention the sources). – Nomenclature and taxonomy of the rust on *E. amygdaloides* remain uncertain. Müller (1907) found only urediniospores on *E. amygdaloides* and consequently did not assign this rust to any of his five collective types. He has shown that his *M. helioscopiae* s.str. (now *M. euphorbiae-helioscopiae*) can attack only *Euphorbia helioscopia*. Nevertheless, Gäumann (1959) and Mayor (1960) used the name *M. helioscopiae* G. Winter f.sp. *amygdaloidis* W. Muell. for the rust on *E. amygdaloides*. Mayor (1958), Brandenburger (1985), Poelt and Zwetko (1997) and Klenke and Scholler (2015) recognised this taxon on species level as *M. euphorbiae-amygdaloidis* W. Muell. – For records of *M. euphorbiae-amygdaloidis* in Austria see Poelt and Zwetko (1997: 77).

***Melampsora euphorbiae* s.l. on *Euphorbia illirica* (*E. austriaca*).** – Spermatogonia and aecia unknown. – Uredinia hypophyllous, scattered, surrounded by the ruptured epidermis. Paraphyses capitate (to clavate); head up to 19–23 µm wide; wall up to 5 µm thick. – Urediniospores globoid to ellipsoid, 18.5–22 × 16–19.5 µm; wall hyaline, about 1.5 µm thick, finely and densely echinulate; distance of spines about 1.5 µm. – Telia hypophyllous, at first minute, scattered, then merging to dark reddish-brown crusts. – Teliospores thin-walled, their spore dimensions correspond to the values given for *M. euphorbiae* s. Gäumann. Our measurements of spores and paraphyses are based on Austrian collections. – *Euphorbia austriaca* and *E. villosa* are now included in *E. illirica*. Gäumann (1959) reported *E. villosa* only as host of *M. euphorbiae-dulcis* without having proven this by inoculation experiments. – *Euphorbia austriaca* in the original circumscription would be endemic in the NE Alps, and collections of the rust are rather common from this area. For records of *M. euphorbiae* s.l. on *E. illirica* (syn. *E. austriaca*) in Austria see Poelt and Zwetko (1997: 77).

***Melampsora euphorbiae* s.l. on *Euphorbia pulcherrima*.** – Spermatogonia and aecia unknown. – Uredinia hypophyllous, scattered or in small groups, minute, 0.3–0.5 mm in diam., yellow-orange, producing pale yellow necrotic spots on the upper surface of the leaf; spots often surrounded by a dark red margin. Paraphyses capitate, head 17.5–22.5 µm wide; wall apically thickened up to 6.5 µm. – Urediniospores subgloboid or ellipsoid, 17.5–21.5(–26.5) × 15.0–19.0 µm; wall 1.5–2.5 µm thick, hyaline, echinulate; contents yellow-orange when fresh. – Telia subepidermal, forming small, dark gray crusts, found in small numbers close to the uredinia. – Teliospores 27–55 × 13–16 µm; wall pale brown, 1.0–1.5 µm thick, apically thickened to 2.5 µm. – Reference: Gjærum et al. (2007: 1–3). In this paper, the authors reported that this rust for the first time caused economic damage on different cultivars of poinsettias (*Euphorbia pulcherrima*) in Norway; the scattered or confluent, necrotic leaf spots reduced the commercial value of the plants considerably. They further stated that it is not known whether the rust

was introduced on imported cuttings or from infected wild *Euphorbia* spp. near the Norwegian greenhouses.

***Melampsora euphorbiae* s.l. on *Euphorbia saxatilis*.** – Spermatogonia, aecia and telia unknown. – Uredinia on both sides of leaves, loosely scattered, surrounded by the ruptured epidermis, rather large. Paraphyses capitate (to clavate); head up to 27–30 µm wide; wall up to 5–8 µm thick. – Urediniospores globoid to ellipsoid, 25–31 × 19–27 µm; wall hyaline, (1.5–)2–2.5 µm thick, finely and densely echinulate; distance of spines about 1.5 µm. Our description is based on one Austrian collection only. – For the occurrence of *M. euphorbiae* s.l. on *E. saxatilis* in Austria see Poelt and Zwetko (1997: 77). The host plant is endemic in the NE Limestone Alps.

***Melampsora euphorbiae* s.l. on *Euphorbia virgata*.** – Spermatogonia and aecia unknown. – Uredinia hypophyllous, occasionally epiphyllous, also on stems, scattered or in groups, on leaves roundish, on stems elongate, surrounded by the ruptured epidermis. Paraphyses capitate (to clavate); head up to 16–21 µm wide; wall up to 3–6 µm thick. – Urediniospores globoid to ellipsoid, 17–21 × 14–16 µm; wall hyaline, about 1.5 µm thick, finely and densely echinulate; distance of spines about 1.5 µm. – Telia hypophyllous, scattered, often merging to dark reddish-brown crusts surrounding the uredinia. – Teliospores thin-walled, their spore dimensions correspond to the values given for *M. euphorbiae* s. Gäumann. Our measurements of spores and paraphyses are based on Austrian collections. Gäumann (1959) reported *E. virgata* as host of *M. euphorbiae-dulcis*, although not without reservation (see below). – For a record of *M. euphorbiae* s.l. on *E. virgata* in Austria see Poelt and Zwetko (1997: 77).

Key to rusts on *Euphorbia*

(Figs 40, 41)

1a Aecia cupulate, with well developed, white peridia. On *Euphorbia amygdaloides* ..... *Endophyllum euphorbiae-sylvaticae*

1b Aecia (if present) cupulate, with well developed, white peridia. Telia pulverulent, dark brown; teliospores occasionally intermixed with few urediniospores. On various *Euphorbia* species, but not on *E. amygdaloides* ..... *Uromyces* spp.

1c Aecia caeomoid, without well-developed peridia, yellow-orange. Uredinia numerous, pulverulent, orange. Telia forming subepidermal or subcuticular crusts consisting of a single layer of spores, at first brownish-orange, then dark brown or black ..... (*Melampsora* spp.) 2

2a Teliospore wall distinctly thickened at apex (up to 5–7 µm) ..... *Melampsora euphorbiae-gerardianae*

2b Teliospore wall evenly thick, or more or less, but not regularly and distinctly thickened at apex 3

3a Teliospores 60–90 × 8–12 µm; wall more or less, but not regularly and distinctly thickened at apex ..... *Melampsora gelmii*

3b Teliospores shorter; wall evenly thick 4

4a Teliospores 40–60 × 7–12 µm ..... *Melampsora euphorbiae-helioscopiae*

4b Teliospores 30–50 × 7–12 µm ..... *Melampsora euphorbiae* s. Gäumann

4c Teliospores 17–35 × 7–15 µm, usually with thicker walls (c. 3 µm) than in *M. euphorbiae-helioscopiae* and *M. euphorbiae* s. Gäumann ..... *Melampsora euphorbiae-dulcis*

16 *Melampsora euphorbiae* (C. Schub.) Castagne s. Gäumann (1959)

Figs 40d, 41a

Syn. *Melampsora euphorbiae* s.l.; *Melampsora euphorbiae* (C. Schub.) Castagne var. *euphorbiae* s. Braun (1982); *M. cyparissiae* W. Muell.; *M. euphorbiae-cyparissiae* W. Muell.; *M. euphorbiae-exiguae* W. Muell.; *M. euphorbiae-pepli* W. Muell.

Auteu-form:

0–III on: *Euphorbia cyparissias*, *E. esula*, *E. exigua*, *E. palustris*, *E. peplus*, *E. verrucosa*, (*E. epithymoides* [syn. *E. polychroma*], *E. lucida*, *E. salicifolia*?, *E. stricta*?)

Spermatogonia subepidermal, flattened hemispherical, orange. – **Aecia** amphigenous, on leaves up to 0.5 mm in diam., on stems up to 4 mm long, orange, without paraphyses. – **Aeciospores** globoid or ellipsoid, 21–28 × 19–24 µm; wall about 1.5 µm thick, densely verrucose. – **Uredinia** usually hypophyllous, sometimes also epiphyllous, rarely on stems, minute, up to 0.5 mm in diam., densely scattered over the leaf but rarely confluent, yellow. Paraphyses numerous, capitate; head 15–20 µm wide. – **Urediniospores** globoid or ellipsoid, 15–22 × 12–20 µm; wall hyaline, ± densely echinulate; contents yellow. – **Telia** subepidermal, on both sides of leaves and on stems, minute but often merging to small crusts, reddish-brown then black. – **Teliospores** cylindrical-prismatic, 30–50 × 7–12 µm; wall 1.5–3 µm thick, reddish-brown or brown, not thickened at apex. – References: Gäumann (1959: 180–181), Wilson and Henderson (1966: 68).

Melampsora euphorbiae s. Gäumann is reported to show three specialised forms (Müller 1907; Gäumann 1959):

- f.sp. *cyparissiae* W. Muell. (syn. *M. euphorbiae-cyparissiae* W. Muell.) on *Euphorbia cyparissias*,

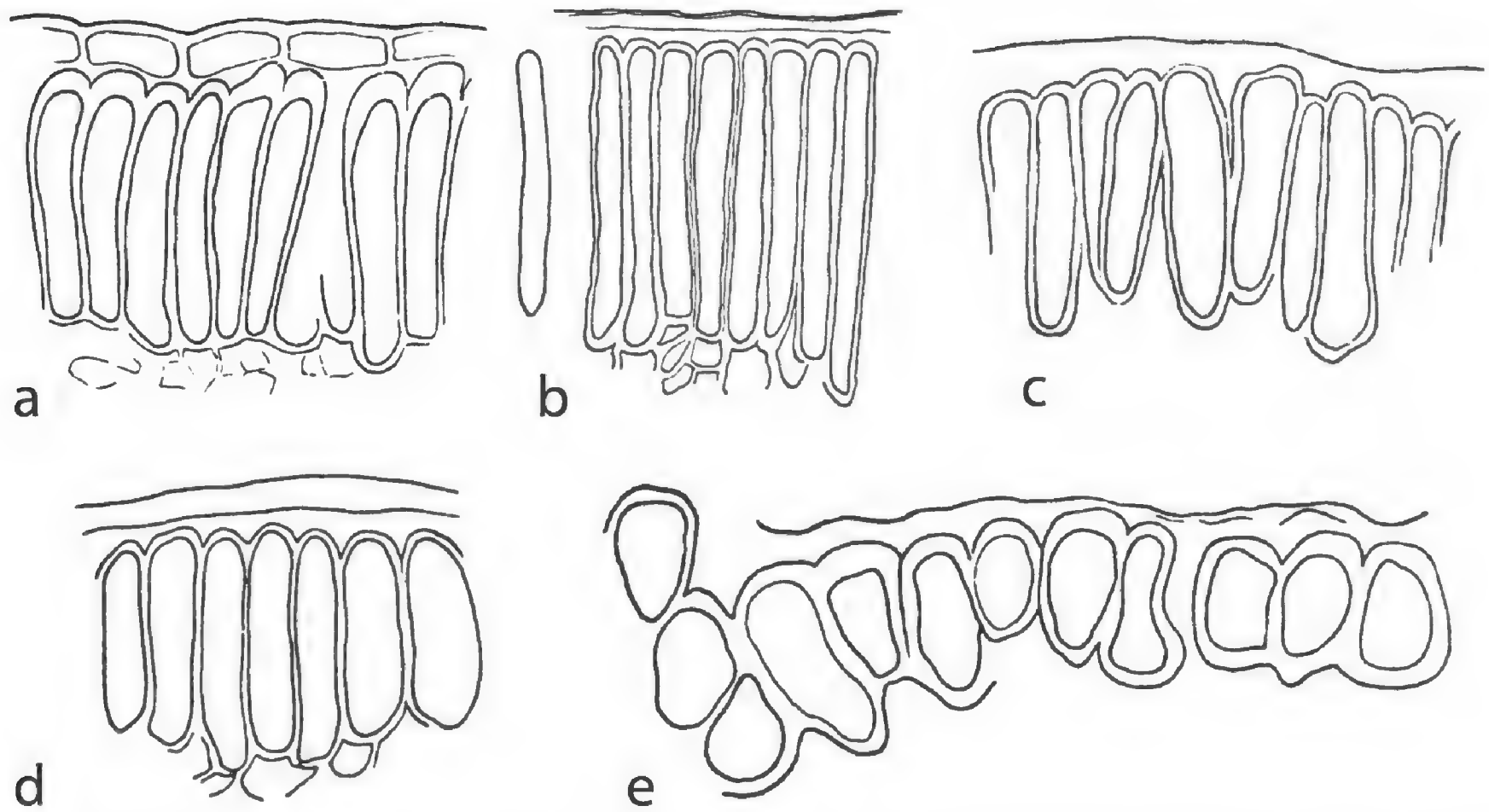


Figure 40. *Melampsora euphorbiae* s.l., teliospores in comparison: **a.** *M. euphorbiae-gerardianae* on *Euphorbia seguieriana*; **b.** *M. gelmii* on *E. terracina*; **c.** *M. euphorbiae-helioscopiae* on *E. helioscopia*; **d.** *M. euphorbiae* s. Gäumann on *E. exigua*; **e.** *M. euphorbiae-dulcis* on *E. dulcis*; (**a–e** from Müller 1907: 548, 546, 552, 553, 558, with permission from Elsevier).

- f.sp. *exiguae* W. Muell. (syn. *M. euphorbiae-exiguae* W. Muell.) on *E. exigua*,
- f.sp. *pepli* W. Muell. (syn. *M. euphorbiae-pepli* W. Muell.) on *E. peplus*.

Remarks. Müller (1907) noticed that rust collections on *Euphorbia esula*, *E. lucida*, *E. palustris* and *E. verrucosa* are morphologically similar to those of f.sp. *cyparissiae*, f.sp. *exiguae* and f.sp. *pepli*. But the host specialisation of these *Euphorbia* rusts remains uncertain. Gäumann (1959) mentioned further *Euphorbia* species as hosts. To our knowledge these records are based on old literature, but Gäumann (l.c.) did not cite the sources. Mayor (1971) reported *Melampsora euphorbiae* (uredinia and telia) on *E. epithymoides* (syn. *E. polychroma*) from Switzerland. He drew attention to the fact that Gäumann (1959) listed this *Euphorbia* species only as host of *M. helioscopiae* (now *M. euphorbiae-helioscopiae*). – The assignment of the Austrian rust collections to *M. euphorbiae* s. Gäumann is based on teliospore morphology. For records of this rust in Austria see Poelt and Zwetko (1997: 77).

17 *Melampsora euphorbiae-dulcis* G.H. Otth

Figs 40e, 42

Syn. *Melampsora euphorbiae* s.l.; *M. euphorbiae* (C. Schub.) Castagne var. *euphorbiae-dulcis* (G.H. Otth) U. Braun; *M. euphorbiae-strictae* W. Muell.

Auteu-form:
0–III on: *Euphorbia angulata*, *E. dulcis*, *E. lathyris*, (*E. carniolica*, *E. platyphyllos*, *E. palustris*?, *E. stricta*, *E. illirica*? [syn. *E. villosa*])
(0,I),II,(III) on: *Euphorbia virgata*?

Spermatogonia amphigenous, hemispherical. – **Aecia** usually hypophyllous, producing red spots on the upper side of leaves, occasionally epiphyllous and on stems, without paraphyses. – **Aeciospores** globoid or ellipsoid, up to 28 µm long, 20–24 µm wide; wall densely verrucose. – **Uredinia** hypophyllous, minute, up to 0.5 mm in diam., on pale yellowish leaf spots, single or in groups, sometimes surrounding a central sorus, orange-yellow. Paraphyses numerous, capitate, head 14–26 µm wide. – **Urediniospores** globoid or ellipsoid, 16–24 × 16–20 µm; wall hyaline, echinulate; contents orange. – **Telia** subepidermal, hypophyllous, occasionally on stems, often merging to large crusts, pale yellow-brown then dark brown but not black. – **Teliospores** cylindrical-prismatic, prismatic or in loose arrangement and then ovoid, 17–35 × 7–15 µm; wall yellowish-brown, rather thick (up to 3 µm), but not thickened at the apex. – Reference: Gäumann (1959: 183).

Melampsora euphorbiae-dulcis is reported to show two specialised forms (Müller 1907; Gäumann 1959):

- f.sp. *dulcis* W. Muell. on *Euphorbia dulcis* and *E. lathyris*,
- f.sp. *strictae* W. Muell. (syn. *M. euphorbiae-strictae* W. Muell.) on *E. platyphyllos* and *E. stricta*.

Remarks. Müller (1907) noticed that rust collections on *Euphorbia carniolica* and *E. virgata* are morphologically similar to those of f.sp. *dulcis* and f.sp. *strictae*. But the host specialisation of these *Euphorbia* rusts remains uncertain. Tranzschel (1927) supposed that Müller (1907) took *E. procera* for *E. virgata*. Gäumann (1959) mentioned further *Euphorbia* species as hosts, but these records are based on

Figure 41. *Melampsora* on *Euphorbia*. **a.** *M. euphorbiae* s. Gäumann on *E. peplus*, orange uredinia and blackish-brown telia on the lower side of leaves; **b.** *M. euphorbiae-helioscopiae* on *E. helioscopia*, close-up; (**b** by Julia Kruse).

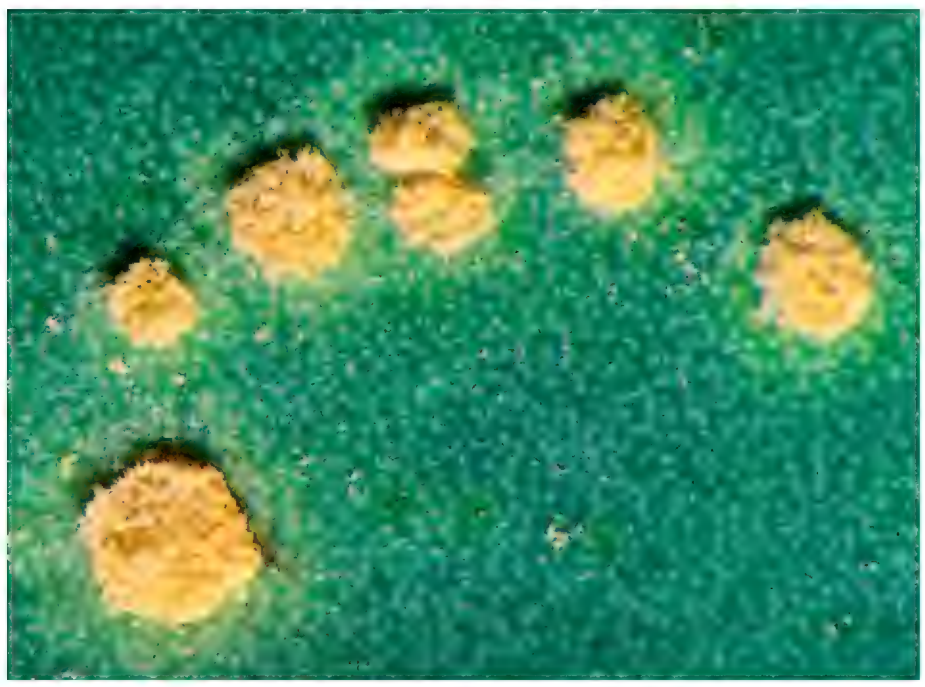


Figure 42. *Melampsora euphorbiae-dulcis* on *Euphorbia lathyris*: uredinia on the lower side of the leaf.

old literature not cited by Gäumann. – The assignment of Austrian collections to *Melampsora euphorbiae-dulcis* is based on teliospore morphology. Because of thin-walled teliospores, we assign all Austrian collections on *E. virgata* to *M. euphorbiae* s.l. (see above). For records of *M. euphorbiae-dulcis* in Austria see Poelt and Zwetko (1997: 78).

18 *Melampsora euphorbiae-gerardianae* W. Muell.

Fig. 40a

Syn. *Melampsora euphorbiae* s.l.

Probably auteu-form:

II,III on: *Euphorbia falcata*, (*E. seguieriana* [syn. *E. gerardiana*])

Spermatogonia and aecia unknown. – **Uredinia** on both sides of leaves and on stems. Paraphyses clavate (to capitate), 40–60 µm long, 16–19 µm wide; wall 4–6 µm thick. – **Urediniospores** mainly globoid or slightly elongate, occasionally polyhedral or pear-shaped, 15–18 × 12–15 µm; wall 1–2 µm thick, echinulate-verrucose; distance of warts 2 µm. – **Telia** subepidermal, on both sides of leaves and on stems, often surrounding the uredinia, especially on stems merging to large crusts (1 cm long), black with brownish margin. – **Teliospores** prismatic, below and at apex somewhat angular, 40–65 × 7–12 µm, gold-coloured, yellow or brownish; wall 2 µm thick at sides, thickened at apex (up to 5–7 µm). – Reference: Gäumann (1959: 184–185).

Remarks. *Melampsora euphorbiae-gerardianae* takes a special position among the *Euphorbia* rusts because it is the only one with pronouncedly apically thickened teliospore walls. – For a record of *M. euphorbiae-gerardianae* in Austria see Poelt and Zwetko (1997: 78).

19 *Melampsora euphorbiae-helioscopiae* (Pers.) Nannf.

Figs 40c, 41b

Syn. *Melampsora euphorbiae* s.l.; *M. euphorbiae* (C. Schub.) Castagne var. *euphorbiae* s. Braun (1982); *M. helioscopiae* (Pers.) G. Winter

Auteu-form:

0–III on: *Euphorbia helioscopia*, (*E. amygdaloides*?, *E. angulata*?, *E. epithymoides*? [syn. *E. polychroma*], *E. glareosa*?)

Spermatogonia subepidermal, flattened-hemispherical. – **Aecia** on leaves up to 0.25–0.5 mm in diam., on stems 1–4 mm long, reddish-orange, without paraphyses. – **Aecio-**

spores globoid or ellipsoid, 21–28 × 19–24 µm; wall about 1.5 µm thick, densely verrucose; distance of warts 1 µm or less. – **Uredinia** roundish or elongate. Paraphyses numerous, capitate; head 17–25 µm wide; wall 4–5 µm thick. – **Urediniospores** globoid, ellipsoid or somewhat polyhedral, 16–22 × 15–18 µm; wall hyaline, 2–2.5 µm thick, ± loosely echinulate; distance of spines 1.5–2 µm. – **Telia** subepidermal, on both sides of the leaves, minute but often confluent, reddish-brown then black. – **Teliospores** prismatic, 40–60 × 7–12 µm; wall brown, thin, not thickened at apex. – Reference: Gäumann (1959: 179).

Gäumann (1959) recognised two specialised forms, although not without reservation:

- f.sp. *helioscopiae* W. Muell. (*M. helioscopiae* s.str. in Müller 1907) on *Euphorbia helioscopia*,
- f.sp. *amygdaloidis* W. Muell. (*M. euphorbiae-amygdaloidis* W. Muell.) on *E. amygdaloides*.

Remarks. After carrying out a number of inoculation experiments, Müller (1907) emphasised that the rust on *Euphorbia helioscopia* did not infect *E. amygdaloides*. He also stated that he found only uredinia on *E. amygdaloides*. For further comments on '*Melampsora euphorbiae-amygdaloidis*' see above under *M. euphorbiae* s.l.

Gäumann (1959) mentioned further *Euphorbia* species as hosts of *Melampsora helioscopiae* (now *M. euphorbiae-helioscopiae*), e.g., *E. pilosa* L. (*E. pilosa* auct. eur. [non L.] is a synonym of *E. villosa*). To our knowledge, these records are based on old literature not cited by Gäumann. – The assignment of the Austrian collections is based on teliospore morphology. For records of *M. euphorbiae-helioscopiae* in Austria see Poelt and Zwetko (1997: 78).

(20) *Melampsora gelmii* Bres.

Fig. 40b

Syn. *Melampsora euphorbiae* s.l.

Probably auteu-form:

(II,III on: *Euphorbia falcata*)

Spermatogonia and aecia unknown. – **Uredinia** on both sides of leaves, but mostly hypophyllous, scattered, 0.5–1 mm in diam., yellow-brown. Paraphyses numerous, clavate to capitate; head 15–20 µm wide. – **Urediniospores** globoid or ellipsoid, 15–25 × 15–23 µm; wall finely echinulate; contents yellow-brown. – **Telia** subepidermal, on both sides of leaves, but mostly hypophyllous, minute, scattered, often confluent, blackish-brown or black. – **Teliospores** cylindrical-prismatic, 60–90 × 8–12 µm, yellow-brown or brown; wall more or less, but not regularly and distinctly thickened at apex. – Reference: Gäumann (1959: 178–179).

Remarks. This rust is not listed in the Austrian rust catalogue (Poelt and Zwetko 1997). It frequently occurs on the mediterranean *Euphorbia dendroides* (Gäumann 1959); on *E. falcata* – an annual species – it is reported from Bulgaria (Denchev 1995).

21 *Melampsora farinosa* (Pers.) J. Schröt.

Figs 28b, 32a, 43, 44

Syn. *Melampsora caprearum* (DC.) Thüm.; *M. laricis-caprearum* Kleb.

Hetereu-form, but the occurrence of forms with facultative host alternation and hemiforms is probable:

(0,I on: *Larix decidua*, *L. kaempferi*, *Pseudolarix amabilis*)

II,III on: *Salix appendiculata*, *S. aurita*?, *S. caprea*, *S.* ×*smithiana*?, (*S. caprea* × *aurita*, *S. cinerea* × *viminalis*, *S.* ×*dasyclados*, *S. purpurea*, *S. repens*?, *S. viminalis*)

II,(III) on: *Salix cinerea*?, (*S. daphnoides*, *S. waldsteiniana*?) – less susceptible hosts

Spermatogonia subcuticular (30–)60–70(–100) µm in diam. approx. 20 µm high. – **Aecia** single or in small groups, up to 1 mm long, pale orange when fresh, producing yellowish spots on needles. – **Aeciospores** globoid, angular-globoid or elongate, 15–25 × 12–17 µm; wall thickness 2 µm with thinner areas, finely verrucose (>4 warts/µm²); warts 0.25 µm in diam.; distance of warts 1 µm or less. – **Uredinia** hypophyllous, producing yellow spots on the upper side of the leaves, at first bigger (1–3 mm in diam.) and single, later on smaller and scattered over the leaf. Paraphyses numerous, capitate, 50–60 µm long; head 18–26 µm wide; wall thickness even, 5(–6) µm; stem 5–6 µm wide. – **Urediniospores** ovoid, round or angular, 14–21 × 13–15 µm; wall 2–2.5 µm thick, with thinner areas, distantly echinulate (0.3 spines/µm²). – Gäumann (1959) described the urediniospore ornamentation as 'distantly echinulate-verrucose; distance of warts 2–2.5 µm'. Our examination of collections from Austria partly confirms Gäumann's description (see Fig. 28b under *M. epitea* s.l., p. 216); the distance of spines was 2–3 µm. – **Telia** epiphyllous, subcuticular, in crusts, individual sori small (1 mm or slightly more) but merging to extensive crusts covering nearly the whole leaf. – **Teliospores** prismatic, rounded below, angular at apex, 30–45 × 7–14 µm; wall thin (1 µm) but extremely thickened at apex (up to 10 µm with slightly eccentric germ pore). – **Basidiospores** orange. – References: Gäumann (1959: 149–150), Helfer (1992: 129).

Melampsora farinosa is reported to show two 'specialised forms' (Gäumann 1959):

- f.sp. *typica* Kleb. infects *Salix caprea* intensely, but *S. aurita* only sparsely,
- f.sp. *grandiflora* Schneid.-Or. infects both *Salix caprea* and *S. aurita* intensely.

Remarks. *Melampsora farinosa* takes a special position in the willow rusts because it is the only one with pronouncedly apically thickened teliospore walls; but identification becomes difficult when only uredinia are present. Collections on *Salix caprea* with rather large (up to 3 mm in diam.), single uredinia probably belong

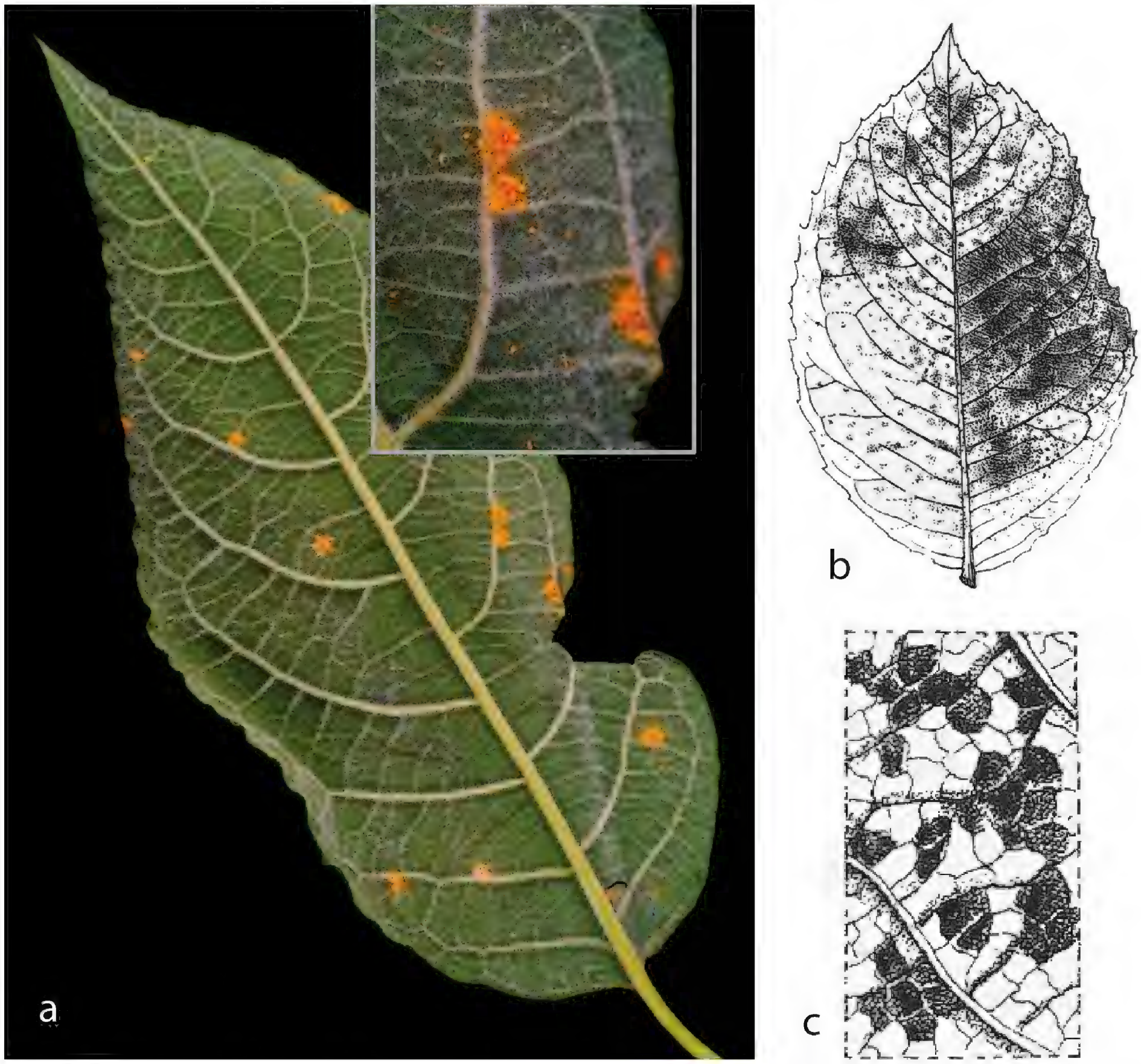


Figure 43. *Melampsora farinosa* on *Salix caprea*: **a.** Orange uredinia on the lower side of the leaves; sori produced at first rather large; **b.** Blackish-brown telia on the upper side of the leaf, confluent into large, irregular crusts; **c.** Telia at higher magnification; (**b, c** from Dietel 1928: 46, as *M. larici-capraearum*, with permission from Duncker & Humblot GmbH).

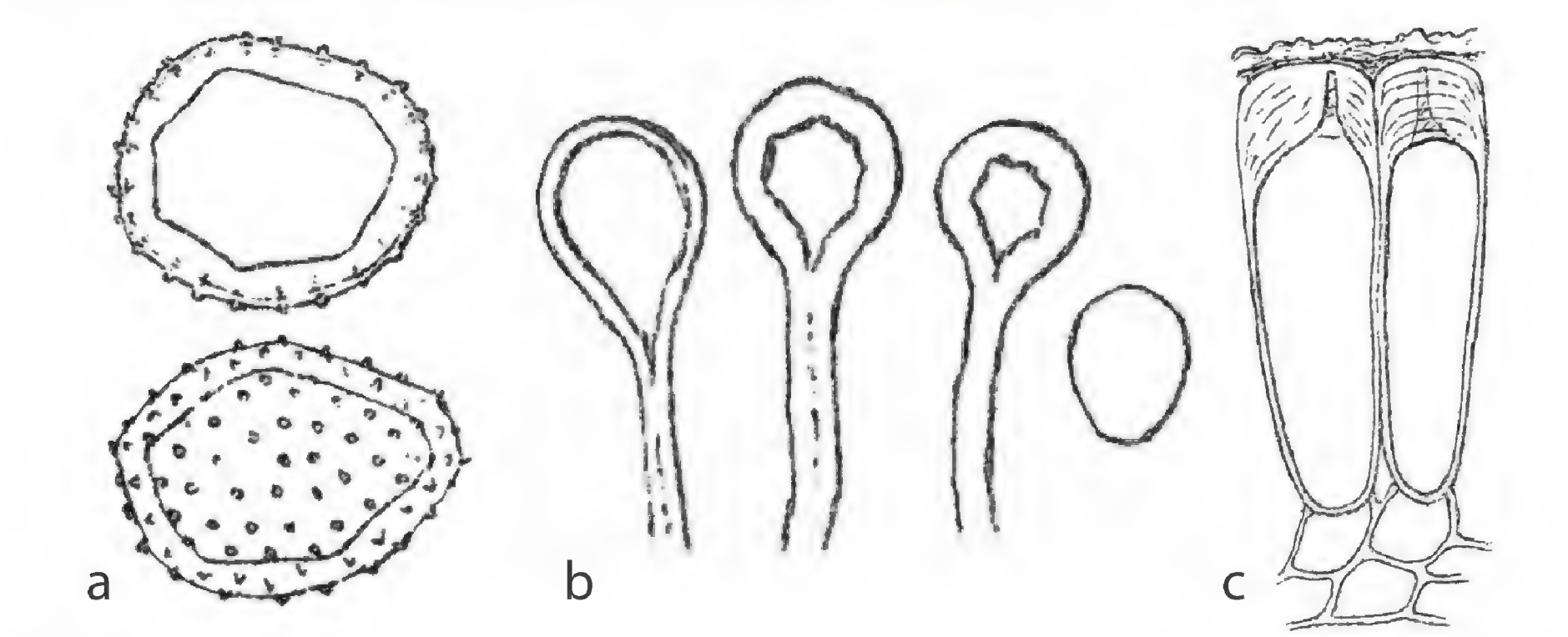


Figure 44. *Melampsora farinosa* on *Salix* ?*caprea*: **a.** Urediniospores evenly echinulate, wall thinner at some spots; **b.** Paraphyses with evenly thick walls, size of an urediniospore in comparison; **c.** Teliospores arranged in subcuticular crust on the upper side of the leaf, spore walls at the apex distinctly thickened; (**a–c** from Klebahn 1914: 794, as *M. larici-capraearum*).

to *M. farinosa*. Uredinia of *M. epitea* s.l. are usually smaller. Telia of *M. farinosa* are epiphyllous and subcuticular, those of *M. epitea* s.l. mainly hypophyllous and subepidermal.

Some mycologists (Klebahn 1914) supposed that the mycelium of the telial stage might survive in *Salix* twigs, but they could not find rust hyphae in the buds of infected twigs. Helfer (1992) emphasises that the rust is very common in Great Britain, both in its aecial and telial stages. According to Wilson and Henderson (1966) and Jørstad (1940), it is probably obligatorily heteroecious in Britain and Norway. But Wilson and Henderson (1966) stated that it is impossible to say, without inoculation experiment, to which species of *Melampsora* any given aecium on larch can be assigned. However, Blumer (1963) used the colour of *Larix* aecia as a character for distinguishing *Melampsora* species in the aecial stage.

Salix caprea × *aurita*, *S. cinerea* × *viminalis*, *S. purpurea*, *S. repens*? and *S. viminalis* have been reported as hosts of *Melampsora farinosa* from Germany (Braun 1982; Brandenburger 1994). To our knowledge these reports are based on old literature (Klebahn 1890b; Engelke 1900; Diedicke 1910). We did not revise herbarium specimens of *M. farinosa* on *S. purpurea*, *S. repens* and *S. viminalis*. In Austria, *M. farinosa* is common in the uredinial and telial stage, but no certain record of the aecial stage is known; therefore, the occurrence of forms with facultative host alternation and hemi-forms can be expected. – For the distribution of *M. farinosa* in Austria see Poelt and Zwetko (1997: 76, as *M. caprearum*).

Key to the *Melampsora* species on *Salix caprea* when only uredinia are present

1a Wall of urediniospores evenly thin (about 1.5 µm thick) and rather densely echinulate (0.6 spines/µm²). Uredinial paraphyses thin-walled (wall 1.5–3 µm thick)..... *M. abietis-caprearum* (*M. epitea* s.l.)
1b Wall of urediniospores thicker (2–4 µm)..... 2
2a Wall of urediniospore 2–2.5 µm thick (with thinner areas), rather distantly echinulate (0.3 spines/µm²). Wall thickness of uredinial paraphyses even (5–6 µm)..... *M. farinosa*
2b Wall of urediniospores 3–3.5 µm thick (with thinner areas), rather distantly echinulate (0.3 spines/µm²). Wall thickness of uredinial paraphyses even (2.5–4 µm, rarely 5 µm)..... *M. ribis-epitea* (*M. epitea* s.l.)
2c Wall of urediniospores 1.5–4 µm thick (with thinner areas), moderately densely echinulate (0.5 spines/µm²). Urediniospores mainly globoid, rarely elongate, 14–19 × 14–17 µm. Wall of uredinial paraphyses often thickened at the apex, up to 8 µm..... *M. euonymi-caprearum* (*M. epitea* s.l.)
2d Wall of urediniospores 1.5–2.5 µm thick but without thin areas, moderately densely echinulate (0.55 spines/µm²). Urediniospores mainly obovoid, often slightly elongate, 12–25 × 9–19 µm. Wall of uredinial paraphyses often thickened at the apex, up to 5–6(–10?) µm..... *M. laricis-epitea* (*M. epitea* s.l.)

22 *Melampsora galanthi-fragilis* Kleb.

Syn. *Melampsora allii-fragilis* Kleb. s.l.; *M. allii-fragilis* Kleb. f.sp. *galanthi-fragilis* (Kleb.) Bagyanarayana

Hetereu-form:
0,I on: *Galanthus nivalis*
(II,III on: *Salix fragilis*, *S. pentandra*)

Spermatogonia flattened hemispherical, 60–100 µm high, 130–160 µm wide. – **Aecia** amphigenous on large, yellowish leaf spots, single or in groups, sometimes confluent to rings surrounding the spermatogonia, bright orange. – **Aeciospores** broadly ovoid or globoid, but usually angular, 17–22 × 14–19 µm; wall 1–2 µm thick, densely and finely verrucose; distance of warts scarcely 1 µm. – **Uredinia** hypophyllous, occasionally epiphyllous, scattered or in groups, 0.5–1 mm in diam., surrounded by ruptured epidermis, bright orange, producing yellow leaf spots. Paraphyses mainly capitate, 50–70 µm long, head 17–23 µm wide; wall thickness even, 2–5 µm. – **Urediniospores** distinctly elongated, often thickened at apex, pear shaped, 25–38 × 12–16 µm; wall thickness 3 µm, with narrow thinner areas (germ pores?), at sides moderately distantly echinulate, smooth at the apex; distance of spines 2–3 µm. – **Telia** mainly epiphyllous, occasionally hypophyllous, in groups or scattered over the surface of the leaf, 0.25–1 mm in size, dark brown, shining. – **Teliospores** irregularly prismatic, ± rounded at both ends, 25–45 × 8–15 µm; wall pale brownish; wall thickness even, 1 µm. – Reference: Gäumann (1959: 161).

Remarks. According to Helfer (1992), *Melampsora galanthi-fragilis* is indistinguishable from *M. allii-fragilis* apart from its aecial host range. Only its aeciospores differ slightly in size and shape from those of *M. allii-fragilis*. See also *Melampsora* sp. 41 (*Caeoma leucoji-verni*, p. 246). – For records of *M. galanthi-fragilis* in Austria see Poelt and Zwetko (1997: 78).

23 *Melampsora hypericorum* (DC.) J. Schröt.

Fig. 54b, c (p. 247)

Syn. *Mesopsora hypericorum* (DC.) Dietel

Probably autopsis-form:
I,III on: *Hypericum hirsutum*, *H. humifusum*, *H. maculatum*, *H. maculatum* agg., *H. montanum*, *H. perforatum*, (*H. dubium*, *H. elegans*, *H. pulchrum*, *H. tetrapterum*)

Spermatogonia lacking. – **Aecia** hypophyllous, caeomoid in appearance but with peridial cells adherent to the upturned host epidermis, without paraphyses, about 0.5 mm in diam., orange, producing yellowish or pale orange spots on the upper side of leaves. – **Aeciospores** in short chains, ellipsoid to polygonal, 15–28 × 10–18 µm; wall thin (1–1.5 µm), hyaline, densely verrucose; distance of warts up to 1 µm; warts 0.25–1 µm wide; contents pale orange. – Uredinia unknown. – **Telia** hypophyllous, subepidermal, on brown leaf spots, minute (0.1 mm in diam.), reddish-brown then dark brown. – **Teliospores** prismatic, rounded at both ends, 20–40 × 7–17 µm; wall pale brownish, 1 µm thick, scarcely thickened above (up to 3 µm). – References: Gäumann (1959: 185–186), Wilson and Henderson (1966: 70).

Remarks. For records of *Melampsora hypericorum* in Austria see Poelt and Zwetko (1997: 78–79). For the rust on cultivated *Hypericum calycinum* and further discussion see under *Melampsora* sp. 46 (p. 247).

(24) *Melampsora laricis-pentandrae* Kleb.

Figs 32d, 45

Hetereu-form:

(0,I on: *Larix decidua*, *L. kaempferi*)

(II,III on: *Salix fragilis* × *pentandra*, *S. pentandra*)

(II on: *Salix fragilis*) – less susceptible host

Spermatogonia bluntly conical, mainly epiphyllous, subcuticular, 60–100 µm in diam., 30–50 µm high. – **Aecia** mainly hypophyllous, single or in small numbers, bright orange, 0.25 × 1 mm in size. – **Aeciospores** in small chains, ovoid, round or slightly angular, 18–26 × 13–20 µm; wall 1.5–2 µm thick, densely verrucose (1.5 warts/µm²). – **Uredinia** mainly hypophyllous, in discoloured spots, 1 mm in diam. Paraphyses capitate or clavate, 40–60 µm long, apex 12–22 µm in diam.; wall thickness even. – **Urediniospores** clavoid, elliptical or ovoid, 26–44 × 12–16 µm; wall about 2 µm thick, distantly echinulate (0.3 spines/µm²), with smooth apex.

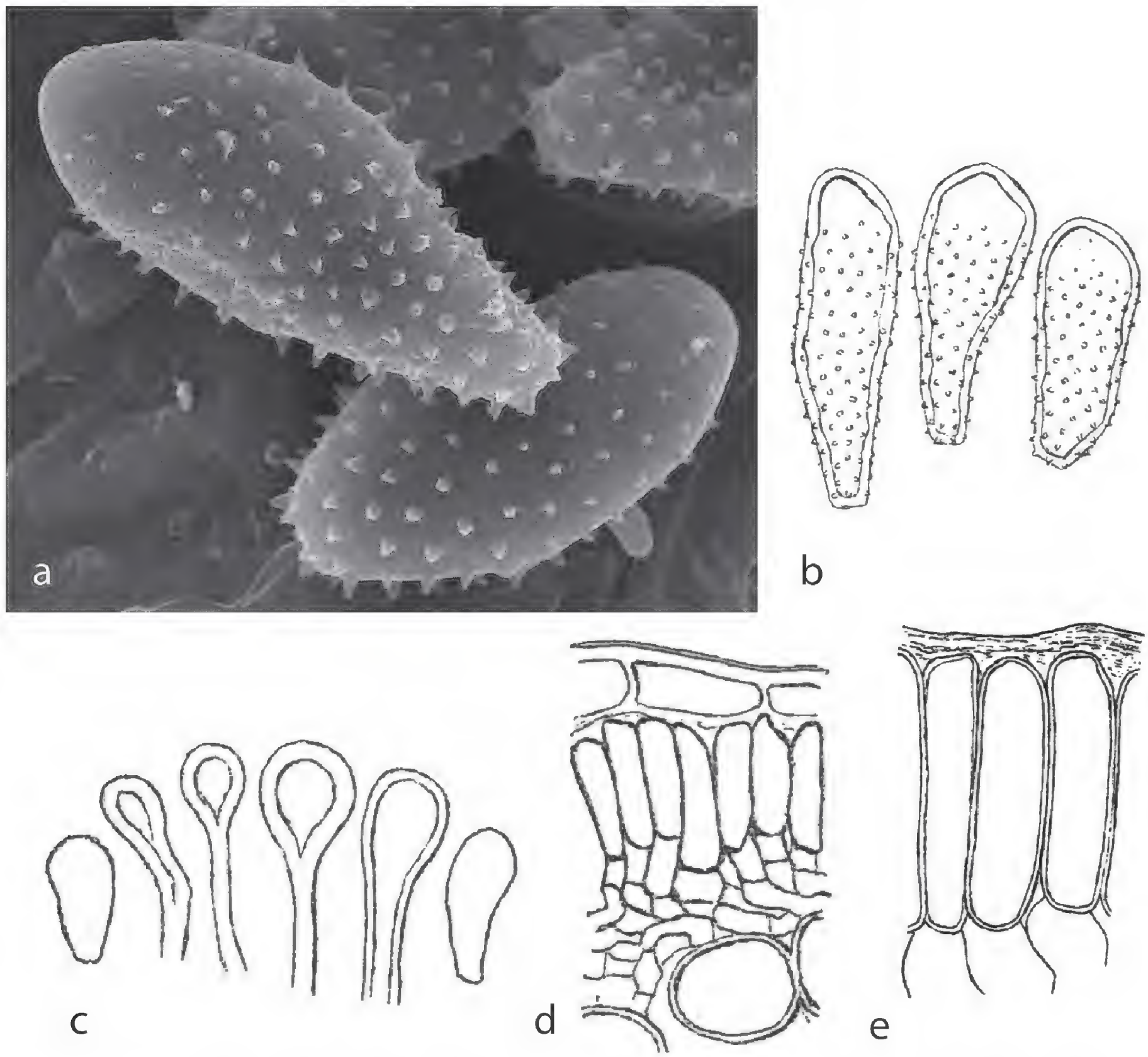


Figure 45. *Melampsora laricis-pentandrae* on *Salix pentandra*: **a.** Urediniospores with smooth apex in SEM; **b.** Urediniospores; **c.** Paraphyses with urediniospores on the same scale; **d.** Subepidermal telium in vertical section; **e.** Teliospores with evenly thick walls; (**a** by Paul Blanz; **b–e** from Klebahn 1914: 782).

– **Telia** hypophyllous, subepidermal, small (0.5 mm), often confluent in crusts covering the whole leaf. – **Teliospores** prismatic, round at the base and slightly angular at the apex, 28–38 × 6–11 µm; wall thickness even, 1 µm. – Reference: Helfer (1992: 130).

Remarks. This rust is reported to survive independent of the alternate host (Jørstad 1960), and may therefore be found in the absence of *Larix*. Taxonomically it is close to *Melampsora amygdalinae*. Its uredinial and telial host range overlaps with that of *M. allii-fragilis*. *Melampsora laricis-pentandrae* has not been found in Austria so far. Despite the rareness of the host *Salix pentandra* in this area, Poelt and Zwetko (1997: 79) assume *M. laricis-pentandrae* to occur here. Due to the difficult identification of both, host and parasite, most of the rusts on *Salix* are less frequently collected than rusts on other hosts.

25 *Melampsora laricis-populina* Kleb.

Figs 32e, 46, 47

Hetereu-form:

(0,I on: *Larix decidua*, *L. kaempferi*)

II,III on: *Populus balsamifera*, *P.* ×*canadensis*, *P. gileadensis*, *P. nigra*, *P. nigra* cv. *italica*, (*P. deltoides*)

Spermatogonia amphigenous, up to 50 µm high and 95 µm wide, yellow. – **Aecia** hypophyllous, in 1 or 2 rows, on slightly yellowish discoloured spots, 0.25–1 mm long, 0.25–0.5 mm wide, yellow-orange, with a rudimentary peridium. – **Aeciospores** globoid or ovoid, 17–22 × 14–18 µm; wall 1.5–2 µm thick, hyaline, finely verrucose, distance of warts less than 1 µm. – **Uredinia** mostly hypophyllous, scattered, often in groups, producing bright yellow, angular spots on the upper side of the leaf, at first covered by the raised epidermis and a hyphal layer, which form rather large pustules and rupture irregularly; spore mass orange. Paraphyses clavate (to capitate), 40–70 µm long, 14–18 µm wide at the apex; wall strongly thickened (up to 10 µm above). – **Urediniospores** distinctly elongated, 30–40(–54) × 13–17 µm; wall about 2 µm thick at the apex and the base, often strongly thickened at the equator (up to 5–6 µm), echinulate except at the smooth apex; distance of spines about 2 µm. Scanning electron micrographs show prickly spines arranged spirally in rows (Siwecki 1990: 99). – **Telia** epiphyllous, subepidermal, minute (less than 1 mm in diam.), but often united in groups and confluent, scattered over nearly the whole leaf, at first red-brown, then blackish-brown. – **Teliospores** prismatic, ± rounded at both ends, 40–70 × 7–10 µm; wall pale, scarcely 1 µm thick, scarcely thickened at the faintly coloured apex (up to 2.5–3 µm). – References: Klebahn (1914: 762–763), Gäumann (1959: 132–133), Wilson and Henderson (1966: 73).

Remarks. According to Frey et al. (2005), three *Melampsora* species, *M. laricis-populina*, *M. allii-populina* and the introduced *M. medusae* are pathogenic on *Populus nigra*, *P. deltoides*, *P. trichocarpa* and their interspecific hybrids (*P.* ×*canadensis* s.l.). Among these three species, *M. laricis-populina* is responsible for most of the economic losses in poplar cultivation in Europe. Therefore, species-specific polymerase chain reaction (PCR) primers and microsatellite markers were developed in order to distinguish *M. laricis-populina* and *M. medusae* in the aecial stage on larch and to distinguish between the three species in the telial stage on fallen poplar leaves (Frey et al. 2005; Steimel et al. 2005). However, the occurrence of *M. medusae* is apparently restricted to W and SW Europe.

Melampsora laricis-populina and *M. allii-populina* distinctly differ in morphology. The former has epiphyllous telia and urediniospores with distinct equatorial thickening; the telia of the latter are hypophyllous, its urediniospores lack such a distinct wall thickening.

We found uredinia and telia of *Melampsora laricis-populina* in Innichen (South Tyrol; altitude about 1100 m). The cultivated *Populus balsamifera* were strongly affected (see Fig. 47), and larch occurred in close vicinity. Therefore, we suppose that host alternation happens. Two other species, *M. laricis-tremulae* and *M. laricis-epitea*, produce aecia on larch. The former infects *Populus alba*, *P. tremula* and their interspecific hybrids, the latter several *Salix* species. Morphology of aeciospores found on larch did not differ sufficiently to distinguish these three *Melampsora* species. They differ only in minute and sometimes hardly detectable details, like arrangement of aecia on the needles, colour of spore mass and size of spores (see Fig. 32 under *M. laricis-epitea*, p. 220). So far, wall ornamentation of aeciospores has not been studied sufficiently.

The effect of the presence of larch on the genetic structure of *Melampsora laricis-populina* populations from wild versus cultivated poplar stands has been investigated by Pinon and Frey (1997) and Frey et al. (2005). The influence of dispersal on the genetic structure of *M. laricis-populina* populations in Europe has been studied by Barrès et al. (2008). The nuclear behaviour in the life cycle of *M. laricis-populina* has been examined by Yu et al. (2009). They observed that germ tubes of urediniospores fused together on the poplar leaf surface, resulting in 4-nucleate and 3-nucleate cells. This new and often temporary association of nuclei may result in gene recombination aside from the usual sexual process. This finding is important. Aecia on larch are rare in Austria, and near-natural sites with both hosts, *Larix decidua* and *Populus nigra*, in close vicinity are lacking in our country. – For records of *M. laricis-populina* in Austria see Poelt and Zwetko (1997: 80).

26 *Melampsora lini* (Ehrenb.) Lév. s.str.

Syn. *Melampsora lini* (Ehrenb.) Lév. var. *lini*, *M. lini* (Schumach.) Desm.

Life cycle insufficiently known:

II,III on: *Linum catharticum*

Spermatogonia and aecia unknown. – **Uredinia** on both sides of the leaves but mostly hypophyllous, also

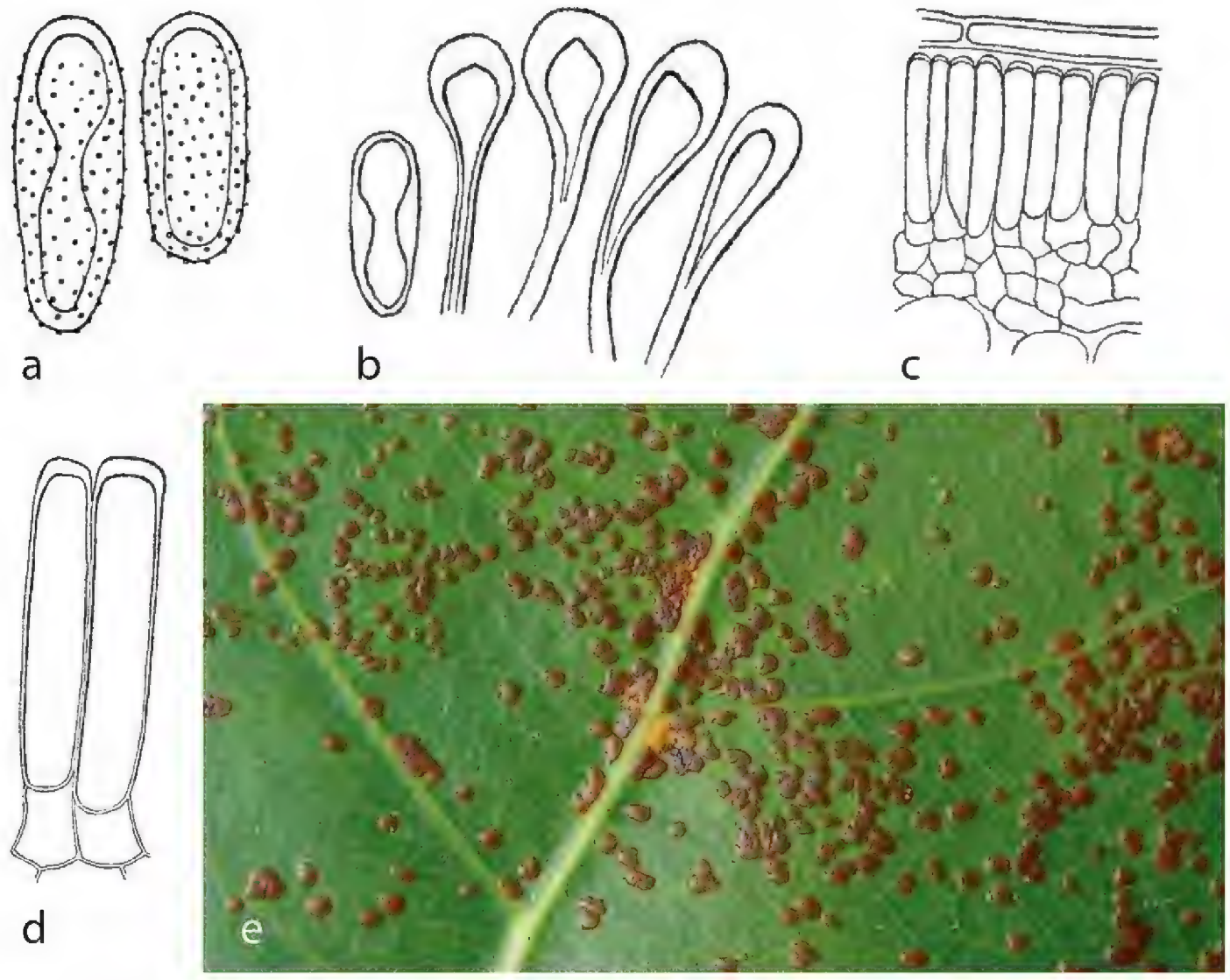
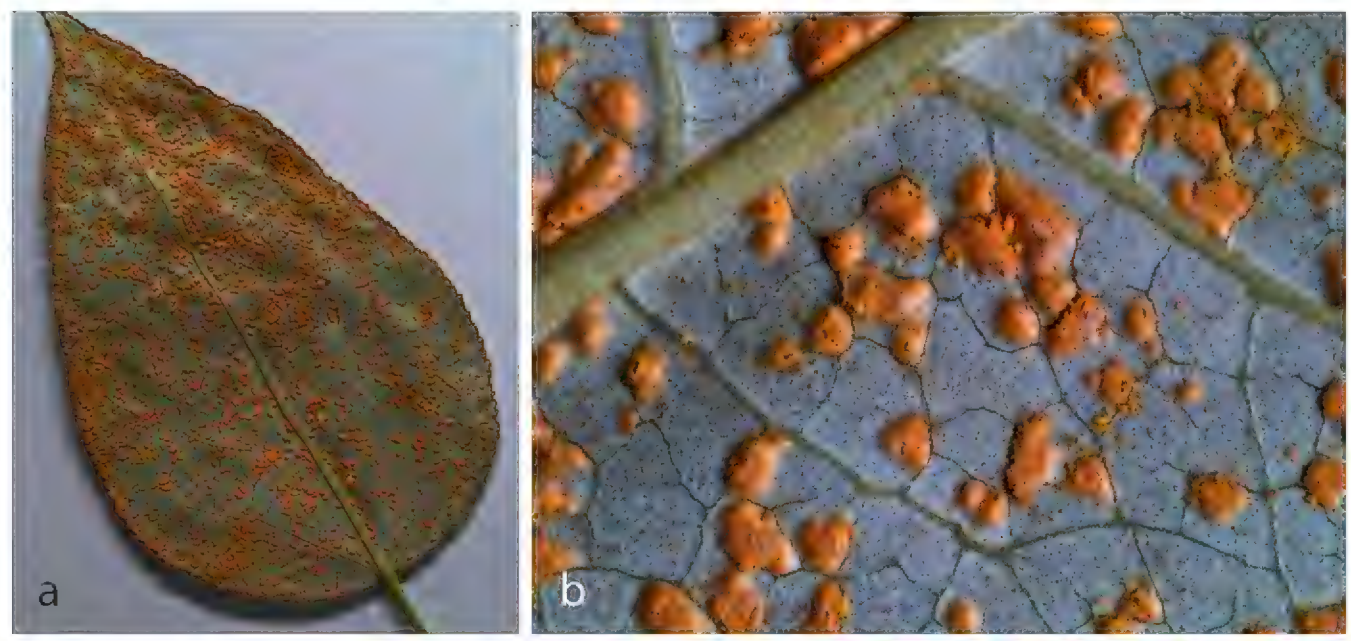


Figure 46. *Melampsora laricis-populina* on *Populus* ×*canadensis*: **a.** Urediniospores with strongly thickened walls at the equator and smooth apex; **b.** Paraphyses with above strongly thickened walls; size of an urediniospore in comparison; **c.** subepidermal telium in vertical section; **d.** Teliospores with scarcely thickened walls at the apex; **e.** Telia epiphyllous; (**a–d** from Klebahn 1914: 766; **e** by Julia Kruse).



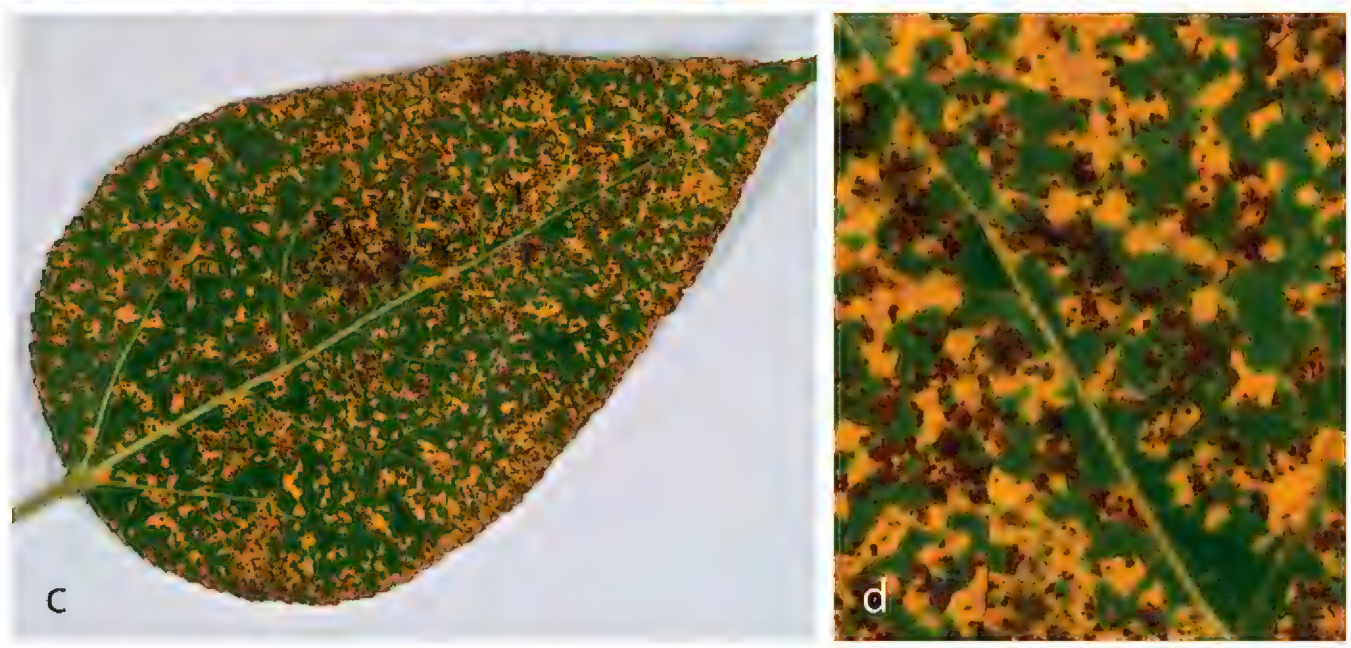


Figure 47. *Melampsora laricis-populina* on *Populus balsamifera*: **a, b.** Uredinia on the lower leaf side; at first forming rather large pustules, then rupturing irregularly and releasing the pulverulent, orange spore mass; **c, d.** Minute, dark reddish-brown telia on the upper leaf side; bright yellow-orange leaf spots indicate uredinia on the lower side.

on stems, scattered or in groups, often crowded, rounded, 0.3–0.75 mm in diam., on stems up to 1.5 mm long, at first covered by the epidermis and a hyphal layer but soon naked, orange. Paraphyses numerous, capitate, 40–50 µm long, 18–23 µm wide; wall 3–6 µm thick. – **Urediniospores** globoid to ellipsoid, (14–)15–19(–23) × 13–18 µm; wall about 1.5 µm thick, hyaline, finely echinulate; distance of spines 1.5–2 µm; germ pores scattered; contents orange-yellow. – **Telia** mostly on stems, also on both sides of leaves, scattered or in groups, often merging to crusts, subepidermal, at first reddish-brown then black and shining. – **Teliospores** cylindrical-prismatic, 35–56 × 7–10 µm, rounded on both ends; wall about 1.5 µm thick and pale brownish at sides, thicker (up to 3 µm) and darker at apex. – References: Gäumann (1959: 193), Wilson and Henderson (1966: 65).

Remarks. According to Gäumann (1959), *Melampsora lini* is strongly specialised to *Linum catharticum*. In NW Europe it overwinters by uredinia (Jørstad 1960; Wilson and Henderson 1966). – For the distribution of *M. lini* s.str. in Austria see Poelt and Zwetko (1997: 80).

Figure 48. *Melampsora liniperda* on *Linum austriacum*: uredinia (photo by Julia Kruse).

27 *Melampsora liniperda* (Körn.) Palm

Fig. 48

Syn. *Melampsora lini* (Ehrenb.) Lév. var. *liniperda* Körn.; *M. lini* (Ehrenb.) Lév. s.l.

Auteu-form:

0–III on: *Linum alpinum* [syn. *L. perenne* subsp. *alpinum*], *L. austriacum*, *L. usitatissimum*, (*L. hirsutum*, *L. flavum*, *L. maritimum*, *L. perenne* s. strictiss., *L. tenuifolium*, *L. viscosum*)

Spermatogonia usually on leaves of seedlings, amphigenous, also on stems, subepidermal, numerous, often in groups, yellow to orange, 63–94 µm high and 97–162 µm wide, flattened globoid and bulging from the leaf as small papillae, causing slight swellings of host tissue. – **Aecia** amphigenous, usually hypophyllous, often in annular or crescentic groups around spermatogonia, 0.25–0.5 mm in diam., orange, with a rudimentary peridium, soon becoming naked and surrounded by ruptured epidermis. – **Aeciospores** globoid or ovoid, (17–)21–25(–27) × (16–)18–22(–24) µm; wall about 1 µm thick, hyaline, densely verrucose (for scanning electron micrographs of mature aeciospores with smooth, knob- or cog-like warts see Gold and Littlefield 1979: 637; the warts are about 1.3 µm tall, but of variable size in cross-section). – **Uredinia** on both sides of the leaves, also on stems, scattered or in groups, rounded or elongated, at first covered by the epidermis and a hyphal layer but soon naked, orange. Paraphyses numerous, capitate, 40–67 µm long, 14–23 µm wide; wall smooth. – **Urediniospores** globoid to ellipsoid, (12–)16–25(–30) × (12–)14–20(–22) µm; wall about 1.5–2 µm thick, hyaline, finely echinulate; contents orange. – **Telia** on stems, fruits and leaves, usually surrounding the uredinia, on leaves scattered, rounded, 0.5–1.5 mm in diam., on stems merging to crusts (up to 25 mm long), subepidermal, at first reddish-brown then black. – **Teliospores** cylindrical-prismatic, (46–)66–72(–81) × (8–)11–14(–19) µm; wall thin and pale brownish at sides, thicker and darker at apex. – For scanning electron micrographs of an anticlinal fracture of a telial crust see Littlefield and Heath (1979: 70); the teliospores are borne on short pedicel-like cells. – References: Gäumann (1959: 190–191), Wilson and Henderson (1966: 65).

Remarks. *Melampsora liniperda* differs from *M. lini* s.str. by its larger uredinio- and teliospores. It occurs on various *Linum* species and is reported to show a number of specialised forms and biotypes (Gäumann 1959). The taxonomy of the whole *M. lini* complex needs revision. According to Wilson and Henderson (1966), the wild species of *Linum* occurring in Europe do not appear to act as hosts for the rust occurring on cultivated flax (*L. usitatissimum*). At present, cultivated flax is rare in Austria. – For records of *M. liniperda* in Austria see Poelt and Zwetko (1997: 81).

28–33 *Melampsora populnea* s.l. (*M. populnea* complex)

28 *Melampsora populnea* s.l.

= *Melampsora populnea* (Pers.) P. Karst. s. Hylander et al. (1953), Wilson and Henderson (1966), Braun (1982)

Accepted species within the complex: ***M. laricis-tremulae***, ***M. magnusiana***, ***M. pinitorqua***, ***M. pulcherrima***, ***M. rostrupii***

Hetereu-forms, forms with facultative host alternation and hemi-forms:

0,I on: *Chelidonium majus*, *Corydalis cava*, *C. intermedia*, *C. solida*, *Larix decidua*, *Mercurialis perennis*, *Pinus sylvestris*, (*Corydalis pumila*, *Fumaria officinalis*, *Larix kaempferi*, *Mercurialis annua*, *Papaver dubium*, *Pinus mugo*, *P. uliginosa* [syn. *P. ×rotundata*])

II,III on: *Populus alba*, *P. tremula*, (*P. ×canescens*)

II,III on: *Populus nigra*?, (*P. nigra* cv. *italica*, *P. balsamifera*, *P. ×canadensis*) – less susceptible hosts

Based on the morphology of urediniospores and paraphyses, the following collection can be assigned to *Melampsora populnea* s.l., but not to any species in the complex:

II on: *Populus alba*

In the latter collection of uredinia on *Populus alba*, the paraphyses are rather thin-walled (1–3 µm) and mostly clavate (Poelt and Zwetko 1997). In the *Melampsora populnea* species complex, the paraphyses are usually capitate and have thicker walls at the head. The species complex is characterised by ovoid, broadly ellipsoid or obovoid urediniospores with uniformly echinulate walls; the teliospores are subepidermal with thin walls which are not thickened at the apex and have no distinguishable germ pore. The rust species included in the complex produce their uredinia and telia on *Populus alba*, *P. tremula* and their hybrids (Frey et al. 2005; Feau et al. 2009). Since aspens and white poplars are not widely cultivated in commercial plantations, the rusts on these species have lower economic importance than *Melampsora laricis-populina* (Frey et al. 2005). Nevertheless *M. pinitorqua* represents an important forest threat due to stem infections on pines, which cause twisting, deformation and death in young trees (Naldini et al. 1992; Feau et al. 2009).

Within the *Melampsora populnea* complex, rust taxa have been usually distinguished as species because they infect different aecial hosts. Longo et al. (1975, 1979, 2002) and Naldini Longo et al. (1985) carried out inoculation experiments on *Larix* and *Pinus* species. They found that *M. laricis-tremulae* and *M. pinitorqua* are different both in their pathogenicity and at least in a few morphological characters. Feau et al. (2009) compared morphometric traits and DNA barcodes in a study on rusts of aspen and white poplar. The combination of three molecular loci in a multigene phylogeny revealed that *M. magnusiana* and *M. rostrupii* are clearly distinct from *M. laricis-tremulae* and *M. pinitorqua*. These two rusts alternate on conifers whereas the aecia of *M. magnusiana* and *M. rostrupii* are found on dicotyledonous plants. Blumer (1963) and Pinon (1973) created keys to rusts on *Populus* species based on the morphology of uredinia and telia.

From the nomenclatural point of view (e.g., MycoBank 2024), *Melampsora populnea* is apparently only a synonym of *M. populina*, a name often used for all *Melampsora* spp. on *Populus*. Here we are retaining the name *M. populnea* as a convenient entity for the species complex, following Hylander et al. (1953).

Key to the *Melampsora* species on *Populus*

(Fig. 49)

1a Urediniospores elongate; wall echinulate at sides, but smooth at apex 2

1b Urediniospores roundish (broadly ellipsoid, ovoid to globoid); wall evenly echinulate. Telia hypophyllous ..... (*M. populnea* s.l.) 3

2a Telia epiphyllous. Wall of teliospores thickened above (2.5–3 µm). Wall of urediniospores about 2 µm thick, but often strongly thickened at the equator (up to 5–6 µm; see **Note 1** below) ..... *M. laricis-populina*

2b Telia amphigenous, but mainly hypophyllous. Wall of teliospores scarcely thickened above (less than 2 µm). Wall of urediniospores 2–4 µm thick, with narrow thinner areas but without equatorial thickening ..... *M. allii-populina*

3a Wall of urediniospores up to 2 µm thick (but in *M. pinitorqua* sometimes thicker at sides, up to 6 µm) 4

3b Wall of urediniospores evenly up to 3 µm thick 5

4a Teliospores 20–35 µm long (see **Note 2** below). Uredinia causing bright yellow spots on the upper side of the leaves; wall of urediniospores sometimes thickened at sides (up to 6 µm) ..... *M. pinitorqua*

4b Teliospores 40–60 µm long (see **Note 2** below). Uredinia causing inconspicuous spots on the upper side of the leaves; wall of urediniospores not thickened at sides ..... *M. laricis-tremulae*

5a Teliospores 25–40 µm long. Uredinia causing bright yellow spots on both sides of the leaves ..... *M. rostrupii*

5b Teliospores (25–)40–50 µm long. Uredinia causing inconspicuous spots on the leaves ..... *M. magnusiana*, *M. pulcherrima*

Note 1 (see also above under *Melampsora laricis-populina*, p. 235): The neomycete ***Melampsora medusae*** Thüm. could potentially be introduced into Austria. It has been recorded in Spain, France, and Portugal (Pinon 1986; Shain 1988). Diagnostic characters after Klenke and Scholler (2015): Urediniospores 26–35 × 15–19 µm; walls echinulate, but smooth and distinctly thickened in the equatorial area; uredinial paraphyses capitate to spathulate, with walls 4–6 µm thick. Telia mostly absent (teliospores 30–45 × 12–15 µm, broader than those of *M. laricis-populina* and *M. allii-populina*). This rust is native in N America, its aecial hosts are *Larix*, *Pinus* and *Pseudotsuga*. Host alternation has not been observed in Europe so far (Klenke and Scholler 2015).

Note 2: According to Naldini Longo et al. (1985), teliospores of *Melampsora laricis-tremulae* are longer and narrower (46.29±10.01 µm) than those of *M. pinitorqua* (40.81±4.71 µm). Walls of uredinial paraphyses are thicker at the apex in *M. pinitorqua* (3–7 µm) than in *M. laricis-tremulae* (3–5 µm).

29 *Melampsora laricis-tremulae* Kleb.

Figs 32f, 49a

Syn. *Melampsora populnea* s.l.; *M. laricis* (Westend.) R. Hartig; *M. populnea* (Pers.) P. Karst. f.sp. *laricis* (R. Hartig) Boerema & Verh.

Hetereu-form and hemi-form:

0,I on: *Larix decidua*, (*L. kaempferi*)

II,III on: *Populus alba*, *P. tremula*, (*P.* ×*canescens*)

(II,III on: *Populus balsamifera*) – less susceptible host

Spermatogonia amphigenous, grouped or slightly scattered, subcuticular, hemispherical to bluntly conical, up to 95 µm wide and up to 50 µm high, pale yellow. – **Aecia** hypophyllous, single or in small groups, rounded or oblong, minute (up to 1 mm long), pale orange, on yellowish spots. – **Aeciospores** globoid, ovoid or angular, 14–17 × 12–16 µm (after Klebahn 1914 and Gäumann 1959), 19.13 (±1.82) × 16.63 (±1.11) µm (after Naldini Longo et al. 1985); wall about 1 µm thick, finely verrucose; distance of warts approx. 1 µm (for scanning electron micrographs of mature aeciospores see Naldini Longo et al. 1985). – **Uredinia** hypophyllous, minute, about 0.5 mm in diam., slightly pulvinate, orange-yellow, on inconspicuous spots. Paraphyses uniformly distributed throughout the sorus, somewhat capitate or clavate, 40–45 µm long, apex 8–17 µm in diam.; wall 3–5 µm thick. – **Urediniospores** ovoid, ellipsoid or obovoid, 15–22 × 10–15 µm (after Klebahn 1914 and Gäumann 1959), 14–23 × 10–16 µm (after Pinon 1973), 23.02 (±1.71) × 19.13 (±1.93) µm (after Naldini Longo et al. 1985); wall about 2 µm thick, echinulate; spines stout, spine distance about 2 µm; germ pores 4–5, mostly bizonate, sometimes scattered. – **Telia** hypophyllous, subepidermal, dark brown, small (up to 1 mm in diam.). – **Teliospores** prismatic, rounded at both ends, 40–60 × 7–12 µm (after Klebahn 1914 and Gäumann 1959), 46.29 (±10.01) × 7.59 (±1.24) µm (after Naldini Longo et al. 1985); wall brownish, evenly thick (1–2 µm), not thickened above, smooth; germ pores not evident. – References: Klebahn (1914: 768–769), Gäumann (1959: 134), Wilson and Henderson (1966: 74–75), Naldini Longo et al. (1985: 437–440), Feau et al. (2009: 717–718).

Remarks. The different aecio- and urediniospore dimensions reported by Klebahn (1914) and Naldini Longo et al. (1985) are due to a different method of preparation. The latter examined spores mounted in lactic acid-phenol.

In the natural environment *Melampsora laricis-tremulae* infects the needles of *Larix decidua*, and *M. pinitorqua* the growing young shoots of several *Pinus* species. The results of artificial inoculations carried out by Longo et al. (1970, 1975) showed that *M. pinitorqua* (collected on *Populus tremula* in Tuscany) is able to infect, besides several species of *Pinus*, also *Larix decidua*, and vice versa that *M. laricis-tremulae* is able to infect, besides *L. decidua*, several species of *Pinus*. For these inoculations seedlings in their first growth cycle with primary needles were used. The two rust fungi differ in urediniospore and teliospore morphology (see key to the rusts on *Populus*, p. 238) and pathogenicity. Therefore, Naldini Longo et al. (1985) considered them as two separate species. Longo et al. (2002) compared the host-parasite interactions between some species of *Pinus* and *M. laricis-tremulae* and the interactions between these same host species and *M. pinitorqua*. The fact that *Pinus pinea* has a lower resistance to *M. laricis-tremulae* than *P. sylvestris* has been attributed to the habitat of *P. pinea*, which is ecogeographically further away from that of *M. laricis-tremulae* than is the habitat of *P. sylvestris*. Thus, *P. pinea* has not been extensively exposed to this rust and has not built up resistance to it. Longo et al. (2002) concluded that *M. laricis-tremulae* and *M. pinitorqua* are closely related; they follow a diverging route of evolution that may eventually lead to their complete separation as distinct species.

Feau et al. (2009) studied *Melampsora* species on aspen and white poplar with DNA barcodes: The delimitation between *M. laricis-tremulae* and *M. pinitorqua* appeared less straightforward than expected. However, the combination of three molecular loci in a multigene phylogeny revealed that *M. magnusiana* and *M. rostrupii* are clearly distinct from *M. laricis-tremulae* and *M. pinitorqua*.

According to Klebahn (1912), the mycelium of *Melampsora laricis-tremulae* can overwinter in poplar buds near Berlin, but its urediniospores did not survive the cold season. This way of overwintering may explain the rarity of aecia on larch in our country. – For records of *M. laricis-tremulae* in Austria see Poelt and Zwetko (1997: 80, as *M. laricis*).

30 *Melampsora magnusiana* G.H. Wagner

Fig. 49d

Syn. *Melampsora populnea* s.l.

Hetereu-form and hemi-form(?):

0,I on: *Chelidonium majus*, *Corydalis cava*, *C. intermedia*, *C. solida*, (*C. pumila*, *Fumaria officinalis*, *Papaver dubium*)

II,(III) on: *Populus alba*?

(II),III on: *Populus tremula*?

II,(III) on: *Populus nigra*? – less susceptible host

Spermatogonia epiphyllous, subepidermal, 130–150 µm wide and 30–40 µm high. – **Aecia** in groups, sometimes confluent (up to 1 mm in diam.), bright orange, on yellowish spots. – **Aeciospores** ovoid or angular, 17–22 × 12–16 µm; wall 1–1.5 µm thick, finely verrucose; distance

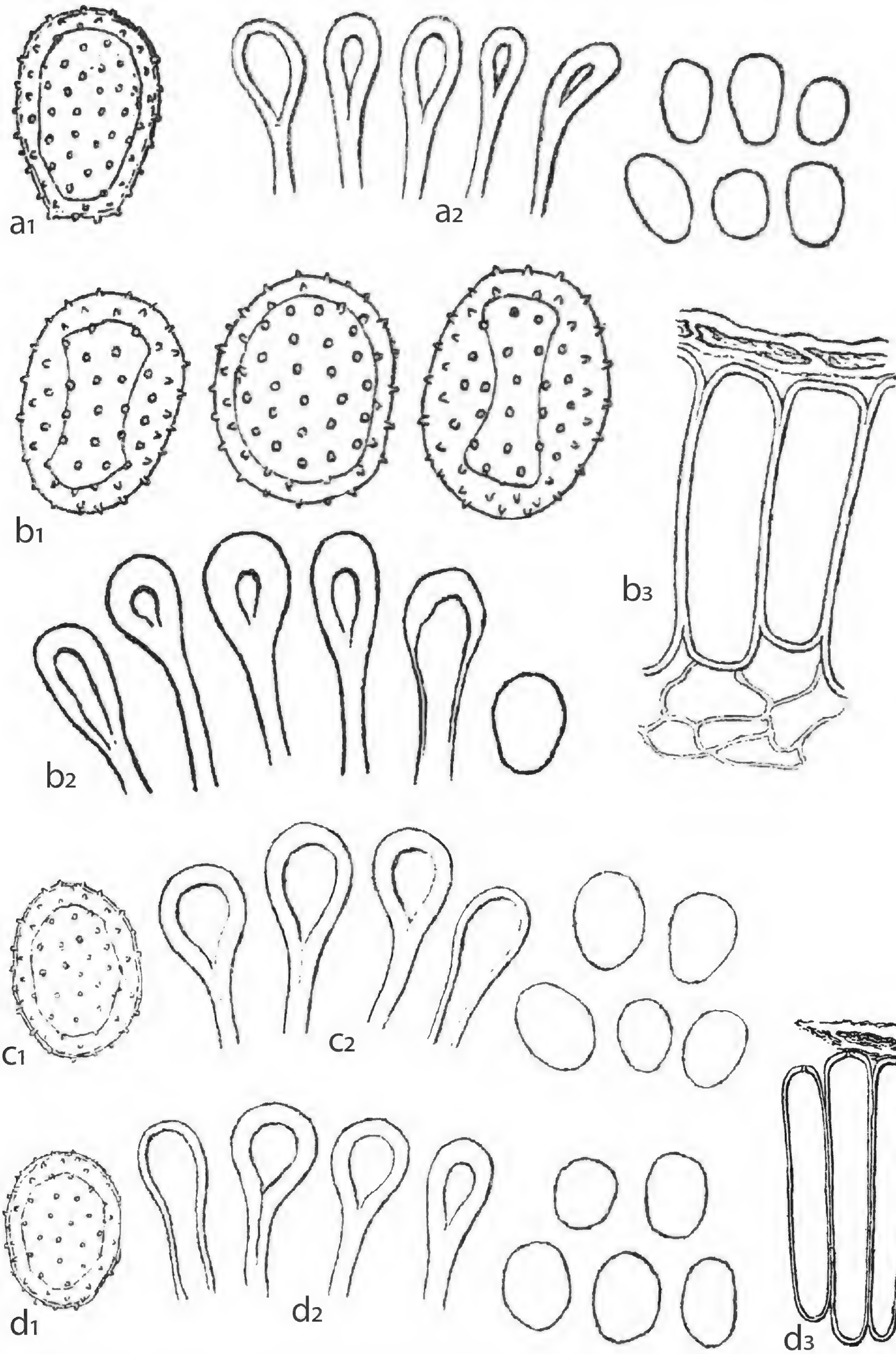


Figure 49. *Melampsora populnea* s.l., urediniospores (1), paraphyses (2, with urediniospores at the same scale for comparison), and teliospores (3): **a1, a2**. *M. laricis-tremulae*, **b1–b3.** *M. pinitorqua*, **c1, c2.** *M. rostrupii*, **d1–d3.** *M. magnusiana*; (**a–d** from Klebahn 1914: 766); for details see the corresponding key (p. 238).

of warts approx. 1 µm. – **Uredinia** hypophyllous, minute, up to 0.5 mm in diam., slightly pulvinate, orange-yellow, on inconspicuous spots. Paraphyses uniformly distributed throughout the sorus, somewhat capitate, occasionally clavate, 40–50 µm long, 14–22 µm wide; wall 3–5 µm thick. – **Urediniospores** ovoid, ellipsoid, obovoid or somewhat angular, 17–24 × 12–18 µm (after Klebahn 1914 and Gäumann 1959), 14–23 × 10–16 µm (after Pinon 1973); wall up to 3 µm thick, echinulate; spines coarse, spine distance 2–3 µm. – **Telia** hypophyllous, subepidermal, dark brown, small (up to 1 mm in diam.). – **Teliospores** prismatic, rounded at both ends, 40–50 × 7–10 µm; wall thickness even (1–2 µm), not thickened above, smooth; germ pores not evident. – References: Klebahn (1914: 774), Gäumann (1959: 142–143), Feau et al. (2009: 717).

Remarks. Feau et al. (2009) studied *Melampsora* species on aspen and white poplar with DNA barcodes: *M. magnusiana* and *M. rostrupii* remained undifferentiated in one single monophyletic clade, but the authors could not rule out the possibility of an incipient differentiation between the two species at the molecular level, as well as in morphological traits (see key to the rusts on *Populus*, p. 238). The combination of three molecular loci in a multigene phylogeny revealed that *M. magnusiana* and *M. rostrupii* are clearly distinct from *M. laricis-tremulae* and *M. pinitorqua*.

Gäumann (1959) drew attention to the fact that in Japan *Chelidonium majus* serves as aecial host for another rust, alternating with *Salix babylonica* which is often cultivated. In Austria, aecia on *Chelidonium* and *Corydalis* are rare. – For records of *M. magnusiana* in Austria see Poelt and Zwetko (1997: 81).

31 *Melampsora pinitorqua* Rostr.

Figs 49b, 50

Syn. *Melampsora populnea* s.l.; *M. populnea* (Pers.) P. Karst. f.sp. *pinitorqua* (Rostr.) Boerema & Verh.

Hetereu-form:

0,I on: *Pinus sylvestris*, (*P. mugo*, *P. uliginosa* [syn. *P.* ×*rotundata*])

II,III on: *Populus alba*?, *P. tremula*, (*P.* ×*canescens*)

Spermatogonia on yellow spots of young shoots, subcuticular or partially subepidermal, punctiform, up to 130 µm wide and 15 µm high, yellow. – **Aecia** erumpent through the cortex of young shoots, occasionally on the leaves, usually single, linear, large (up to 20 mm long and 3 mm wide), reddish-orange. – **Aeciospores** globoid or ovoid, 14–20 × 13–17 µm (after Klebahn 1914 and Gäumann 1959), 19.28 (±1.98) × 16.65 (±1.46) µm (after Naldini Longo et al. 1985); wall about 2 µm thick, but sometimes thicker (up to 4 µm) and then with thin areas, finely verrucose; distance of warts approx. 1 µm (for scanning electron micrographs of mature aeciospores see Naldini Longo et al. 1985). – **Uredinia** hypophyllous, single or in groups, often covering the whole surface, minute, about 0.5 mm in diam., pulvinate, orange-yellow, causing yellow spots on the upper side of the leaf. Paraphyses uniformly distributed throughout the sorus, somewhat capitate (or clavate), 40–50 µm long, 12–17 µm wide; wall of the head 3–7 µm thick. – **Urediniospores** usually ovoid, 15–22 × 11–16 µm (after Klebahn 1914 and Gäumann 1959), 14–24 × 10–16 µm (after Pinon 1973), 23.84 (±1.99) × 18.96 (±1.55) µm (after Naldini Longo et al. 1985); wall about 2 µm thick, but sometimes thicker at sides (up to 6 µm) and then with thin areas beside the thickened areas, echinulate; spines stout, spine distance about 2–3 µm; germ pores 4–5, mostly bizonate, sometimes scattered. – **Telia** hypophyllous, subepidermal, often in groups, brown, not shining, small (about 0.5 mm in diam.). – **Teliospores** irregularly prismatic, rounded at both ends, 20–35 × 7–11 µm (after Klebahn 1914 and Gäumann 1959), 40.81 (±4.71) × 8.22 (±1.36) µm (after Naldini Longo et al. 1985); wall pale brownish, evenly thick (about 1 µm), not thickened above, smooth; germ pores not evident. – References: Klebahn (1914: 770–771), Gäumann (1959: 136), Wilson and Henderson (1966: 76–77), Naldini Longo et al. (1985: 437–440), Feau et al. (2009: 717–718).

Remarks. The different aecio- and urediniospore dimensions reported by Klebahn (1914) and Naldini Longo et al. (1985) are due to a different method of preparation. The latter examined spores mounted in lactic acid-phenol. Their specimens were collected on *Populus tremula* in Tuscany (Italy) and on artificially inoculated *Pinus pinea*, *P. pinaster* and *P. sylvestris*.

Melampsora pinitorqua infects the young long shoots of pines. Main symptoms are bending and twisting shoots in the upper crown. The shoots can break, growth and timber quality can be reduced. Therefore, this rust is highly destructive in pine plantations in Europe. It occurs from Italy to Sweden and from France to Russia (Naldini et al. 1992; Feau et al. 2009). Foresters attempt to eliminate aspen in vicinity of pines (500 m distance).

Molecular data (Feau et al. 2009) and results of inoculation experiments (Naldini Longo et al. 1985; Longo et al. 2002) indicate that *M. pinitorqua* and *M. laricis-tremulae* are closely related. Artificial inoculations resulted in overlapping aecial host ranges of the two rust taxa. *Pinus sylvestris* (the most important host of *M. pinitorqua*) was identified as a 'non-host' of *M. laricis-tremulae*. For more information on the taxonomic relationship of these rusts see remarks on *M. laricis-tremulae*.

For records of *Melampsora pinitorqua* in Austria see Poelt and Zwetko (1997: 81).

(32) *Melampsora pulcherrima* (Bubák) Maire

Syn. *Melampsora populnea* s.l.

Hetereu-form:

(0,I on: *Mercurialis annua*)

(II,III on: *Populus alba*)

Spermatogonia 140–200 µm in diam., at first yellow to honey-coloured then brownish. – **Aecia** roundish to linear,

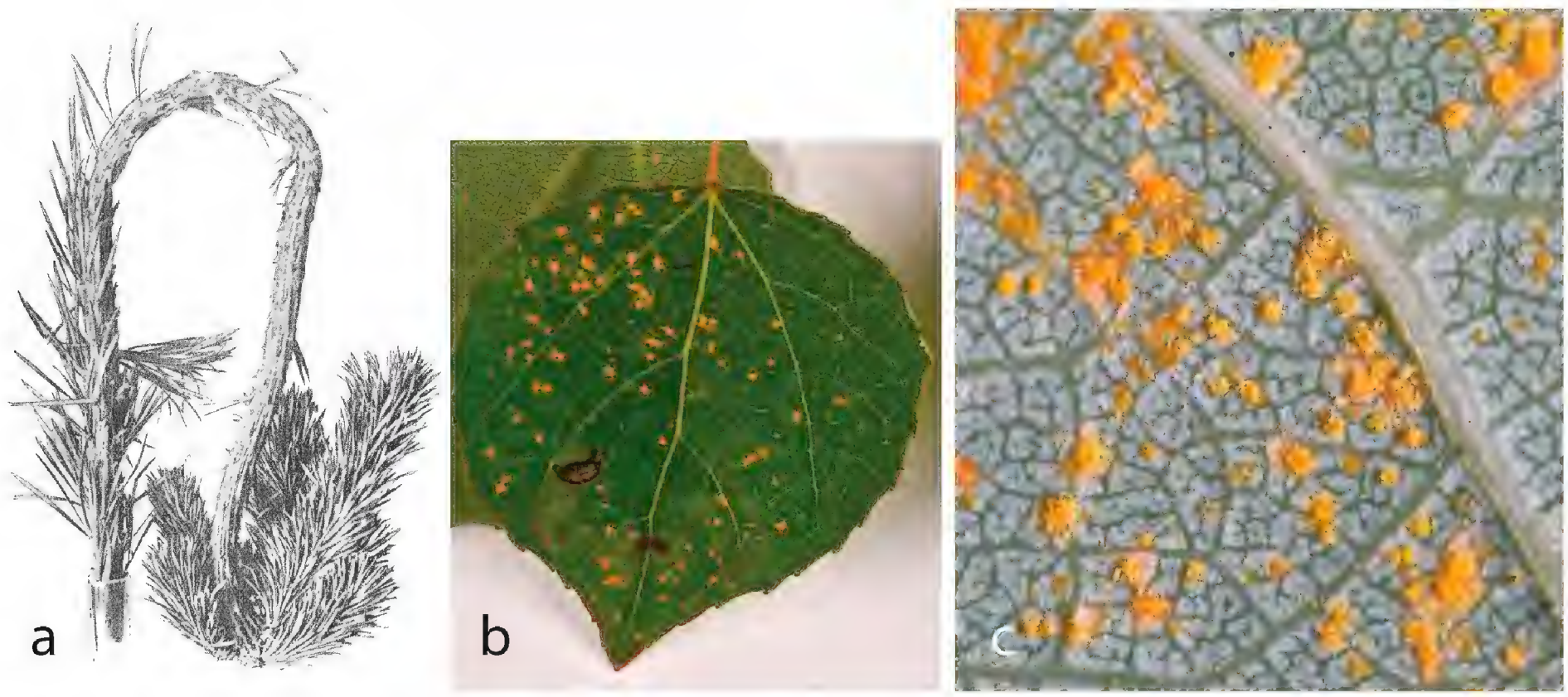


Figure 50. *Melampsora pinitorqua*. **a.** Twisting shoot of *Pinus* sp. caused by aecia-producing mycelium; **b–c.** On *Populus tremula*: **b.** Spots on the upper side of the leaf caused by the uredinia; **c.** Pulverulent uredinia and young telia waxy in appearance; (**a** from Migula 1917: Taf. X/1).

densely arranged and confluent, often covering the surface all around the stem (areas 2–10 cm long), orange. – **Aeciospores** usually globoid to ellipsoid, 15–29 × 15–22 µm; wall rather thin, hyaline, densely and finely verrucose; contents orange. – **Uredinia** usually hypophyllous, minute, up to 0.8–1 mm in diam., yellow-orange, on inconspicuous spots. Paraphyses uniformly distributed throughout the sorus, clavate to capitate, 35–50 µm long, 18–25 µm wide; wall hyaline, thickened at the apex (up to 4 µm). – **Urediniospores** ovoid or globoid, 18–23 × 14–18 µm; wall up to 2.5 µm thick, hyaline, echinulate; contents yellow-orange. – **Telia** hypophyllous, reddish-brown, minute (0.1–0.8 mm in diam.); leaf spots inconspicuous or lacking. – **Teliospores** prismatic, rounded at both ends, 25–50 × 7–9 µm; wall thin, not thickened above, smooth, reddish-brown. – Reference: Gäumann (1959: 141–142).

Remarks. According to Gäumann (1959), the occurrence of *Melampsora pulcherrima* is restricted to S Europe. It has not been found in Austria so far (Poelt and Zwetko 1997). However, its host plants are common in the warmer regions of our country, and Moesz (1941) and Urban and Marková (2009) reported one collection of *M. pulcherrima* on *Mercurialis annua* from Slovakia (near Bratislava).

33 *Melampsora rostrupii* G.H. Wagner

Figs 49c, 51

Syn. *Melampsora populnea* s.l.; *M. populnea* (Pers.) P. Karst. f.sp. *rostrupii* (G.H. Wagner ex Kleb.) Boerema & Verh.

Hetereu-form:

0,I on: *Mercurialis perennis*
II,III on: *Populus alba*, *P. tremula*, (*P.* ×*canescens*)
II,III on: *Populus nigra*?, (*P. nigra* cv. *italica*, *P. balsamifera*, *P.* ×*canadensis*) – less susceptible hosts

Figure 51. *Melampsora rostrupii* on *Mercurialis perennis*: few spermatogonia surrounded by confluent aecia on the lower side of the leaf.

Spermatogonia epiphyllous, occasionally hypophyllous, in small clusters, subepidermal, lenticular, 110–190 µm wide and 45–70 µm high, honey-coloured. – **Aecia** mainly hypophyllous, sometimes on the petioles and stems, about 1–1.5 mm in diam., often in circular groups around the spermatogonia, often confluent, bright orange, on pale yellowish leaf spots. – **Aeciospores** ovoid or globoid-angular, 13–20 × 12–16 µm; wall 1–1.5 µm thick, hyaline, finely and densely verrucose; warts about 1 µm in diam.; distance of warts 1–1.5 µm. – **Uredinia** hypophyllous, rather large, up to 1 mm in diam., pulvinate, producing large, yellow spots on both sides of the leaf. Paraphyses uniformly distributed throughout the sorus, somewhat capitate, occasionally clavate, about 50 µm long, 15–23 µm wide; wall 3–6 µm thick. – **Urediniospores** ovoid, roundish or somewhat angular, 18–25 × 14–18 µm (after Klebahn 1914 and Gäumann 1959), 17–28 × 14–18 µm (after Pinon 1973); wall up to 3 µm thick, echinulate; spine dis-

tance 2–3 µm. – **Telia** hypophyllous, subepidermal, dark brown, small (scarcely 1 mm in diam.). – **Teliospores** prismatic, rounded at both ends, 25–40 × 5–12 µm; wall scarcely 1 µm thick, not thickened above, smooth, pale yellowish; germ pores not evident. – References: Klebahn (1914: 768–769), Gäumann (1959: 139–140), Wilson and Henderson (1966: 76), Feau et al. (2009: 772–773).

Remarks. Feau et al. (2009) studied *Melampsora* species on aspen and white poplar with DNA barcodes: *M. magnusiana* and *M. rostrupii* remained undifferentiated in one single monophyletic clade, but the authors could not rule out the possibility of an incipient differentiation between the two species at the molecular level, as well as in morphological traits (see key to the rusts on *Populus*, p. 238). The combination of three molecular loci in a multigene phylogeny revealed that *M. magnusiana* and *M. rostrupii* are clearly distinct from *M. laricis-tremulae* and *M. pinitorqua*. – Aecia have been frequently found in our country. For records of *M. rostrupii* in Austria see Poelt and Zwetko (1997: 83).

34 *Melampsora ribis-viminalis* Kleb.

Fig. 52

Hetereu-form:

(0,I on: *Ribes alpinum*, *R. aureum*, *R. nigrum*, *R. rubrum*, *R. sanguineum*, *R. uva-crispa*, *R. uva-crispa* subsp. *grossularia*)

II,III on: *Salix viminalis*

Spermatogonia epiphyllous, projecting, forming cushions, 150 µm in diam., 70 µm high. – **Aecia** hypophyllous, in discoloured spots, erumpent in groups, vividly orange, 1.5 mm. – **Aeciospores** mainly roundish, rarely ovoid, few angular, 18–23 × 14–17 µm; wall thickness 2–3 µm, thinner or thicker (up to 4 µm) in some areas, densely and finely verrucose (approx. 4 warts/µm²); distance of warts less than 1 µm. – **Uredinia** hypophyllous, very small (up to 0.25 mm), in groups or spread over the leaf, faintly orange-yellow. Paraphyses mainly clavate with thick stem, also capitate with slender stem, 50–70 µm long, head 18–25 µm wide; wall thickness mainly even, 1–2 µm, sometimes slightly thicker at the head. – **Urediniospores** mainly roundish, rarely ovoid, 15–19 × 14–16 µm; wall thickness 2 µm, distantly echinulate (0.4 spines/µm²); distance of spines about 2 µm. – **Telia** epiphyllous, subcuticular, small (0.25–0.5 mm), scattered over the whole leaf surface, often in groups, dark brown, shining. – **Teliospores** prismatic, rounded at both ends, ± irregular, 25–40 × 7–14 µm; wall thickness even, 1 µm. – References: Gäumann (1959: 166–167), Helfer (1992: 133).

Remarks. Brandenburger (1985, 1994) mentioned *Melampsora epitea* Thüm. var. *epitea* as a synonym for this species, probably by error. *Melampsora ribis-viminalis* is taxonomically fairly distinct from the other rusts occurring on willows (Helfer 1992). It may cause economic losses in biomass energy plantations. – For records of *M. ribis-viminalis* in Austria see Poelt and Zwetko (1997: 83).

Salix viminalis has been reported as host of at least four *Melampsora* species; Braun (1982) listed it also as host of *M. farinosa*. To our knowledge his report is based on old literature (Diedicke 1910). We did not revise herbarium specimens of *M. farinosa* on *S. viminalis*.

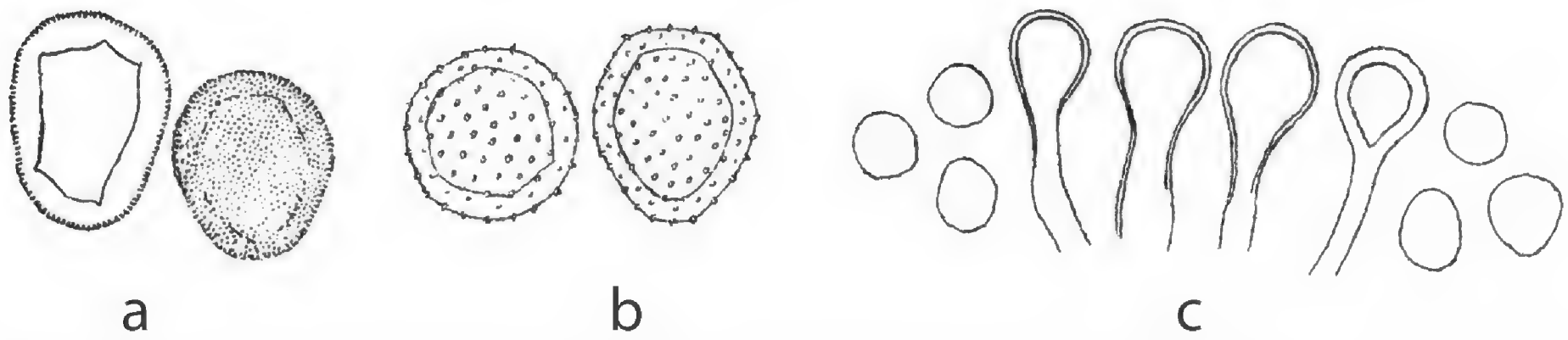


Figure 52. *Melampsora ribis-viminalis*. **a.** On *Ribes rubrum*: aeciospores. **b, c.** On *Salix viminalis*: **b.** Urediniospores; **c.** Paraphyses with rather thin walls (with spores to the same scale); (**a–c** from Klebahn 1914: 794).

Key to the *Melampsora* species on *Salix viminalis*

1a	Telia mainly epiphyllous, subcuticular	2
1b	Telia mainly hypophyllous, subepidermal	(*M. epitea* s.l.) 3
2a	Teliospore wall uniformly thin (about 1 µm)	*M. ribis-viminalis*
2b	Teliospore wall pronouncedly thickened at the apex (up to 10 µm); – uncertain host-parasite combination(!)	*M. farinosa*
3a	Wall of urediniospores about 1.5 µm thick. Wall of uredinial paraphyses 1.5–3 µm thick	*M. abietis-caprearum*
3b	Wall of urediniospores (2–)2.5–3.5 µm thick	4
4a	Uredinial paraphyses with apically thickened walls (up to 5–10 µm)	*M. laricis-epitea*
4b	Wall thickness of uredinial paraphyses even (1.5–4 µm)	5
5a	Wall of urediniospores about 2.5 µm thick with thin areas, moderately densely echinulate (0.6 spines/µm²); – uncertain host-parasite combination(!)	*M. ribis-purpureae*
5b	Wall of urediniospores 3–3.5 µm thick with thin areas, distantly echinulate (0.3 spines/µm²); – uncertain host-parasite combination(!)	*M. ribis-epitea*

35 *Melampsora vernalis* Niessl

Syn. ?*Caeoma saxifragarum* (DC.) Link

Autopsis-form:

0,I,III on: *Saxifraga granulata*

Spermatogonia hypophyllous, scattered, about 75 µm high, about 180 µm wide, honey-coloured. – **Aecia** hypophyllous or on the calyx, roundish, 0.25–0.75 mm in diam., single or evenly distributed over the leaf surface, yellow-orange. – **Aeciospores** ovoid or angular-globoid, (16–)20–26(–34) × (14–)18–22(–28) µm, mean 24.0 × 20.8 µm; wall up to 2 µm thick, hyaline, densely and minutely verrucose; distance of warts less than 1 µm; contents orange. – **Telia** amphigenous, mostly hypophyllous on the lower leaves and stems, subepidermal, minute (0.05 mm) or up to 0.5 mm in diam., at first yellowish then brown or blackish-brown; the minute sori often under the stomata. – **Teliospores** in the larger sori palisade-like, 24–50 × 9–14 µm; teliospores in the minute sori variable in size and shape, clavoid, ± ovoid or roundish, 17–30 × 17–25 µm; wall yellowish-brown, 1.5–2 µm, at apex up to 3 µm thick, with ± evident germ pore. – References: Gäumann (1959: 188–189), Wilson and Henderson (1966: 67).

Remarks. *Melampsora vernalis* is widely distributed in N Europe, as is the related species *M. hirculi* Lindr. on *Saxifraga hirculus*. A single collection of *M. vernalis* from Upper Austria is reported by Poelt and Zwetko (1997: 84). *Melampsora hirculi* was probably not present in the major part of Central Europe before its host disappeared. Based on old literature, Urban and Marková (2009) reported *Saxifraga caespitosa* as another host of *M. vernalis* from Bohemia. However, this report seems doubtful.

36 *Melampsora vitellinae* (DC.) Thüm.

Fig. 53

Syn. *Melampsora allii-salicis-albae* Kleb.; *M. salicis-albae* Kleb.

Hetereu-form:

0,I on: *Allium flavum*, *A. ursinum*, (*A. ascalonicum*, *A. carinatum*, *A. cepa*, *A. fistulosum*, *A. ochroleucum*, *A. oleraceum*, *A. pulchellum*, *A. rotundum*, *A. sativum*, *A. schoenoprasum*, *A. scorodoprasum*, *A. lusitanicum* [syn. *A. senescens* subsp. *montanum*], *A. sphaerocephalum*, *A. strictum*, *A. suaveolens*, *A. victorialis*, *A. vineale*)

II,III on: *Salix alba*, (*S. alba* × *babylonica*, *S. alba* × *fragilis*, *S. alba* × *triandra*, *S. pentandra*, *S. retusa*)

Spermatogonia protruding slightly, 210 µm in diam., approx. 120 µm high. – **Aecia** on leaves and stems, in groups, in the centre of yellow spots; individual sori 1 mm in diam., bright orange-yellow. – **Aeciospores** irregular, mainly angular and isodiametrical, rarely elongated, 17–26 × 15–18 µm; wall 1–1.5 µm thick, densely and finely verrucose (approx. 4 warts/µm²); distance of warts scarcely 1 µm. – **Uredinia** of two kinds: (1) in spring erumpent from the cortex of young twigs and as much as 5 mm long, then on young leaves and on scales of recently opened buds, up to 2 mm long and densely crowded; (2) in summer and autumn on the leaves, mainly hypophyllous, small (0.5 mm), producing inconspicuous spots. Paraphyses mainly capitate, occasionally clavate, 50–70 µm long, head 15–20 µm wide; wall thickness even, 2–3 µm; paraphyses absent from cortical sori. – **Urediniospores** in all kinds of sori similar, pronouncedly elongated, sometimes clavate or pyriform, 20–36 × 11–17 µm; wall 2 µm thick, smooth at the apex, otherwise distantly echinulate (0.35–0.4 spines/µm²); distance of spines 2–2.5 µm. – **Telia** amphigenous, often epiphyllous, subepidermal, small, scattered thinly over the leaf surface, singly or in groups, dark brown. – **Teliospores** irregularly prismatic, rounded at both ends, 25–45 × 7–10 µm; wall scarcely 1 µm thick, not thickened above, without evident germ pore. – References: Gäumann (1959: 160–161), Wilson and Henderson (1966: 91), Helfer (1992: 133).

Remarks. This rust is quite frequent in Europe and can persist without host alternation. It can winter by the mycelium in the cortex of the branches on which uredinia are produced before aecia appear in spring (Klebahn 1938). *Melampsora vitellinae* is of economic importance as it renders basket willows unsuitable for this purpose (Helfer 1992).

The telial host range of *Melampsora vitellinae* is remarkable. It includes *Salix alba* and *S. retusa*; the former is a 5–30 m tall tree growing in riparian forests of the lowlands and higher valleys (altitudes 700–800 m), the latter is a 10 cm high willow of the subalpine and

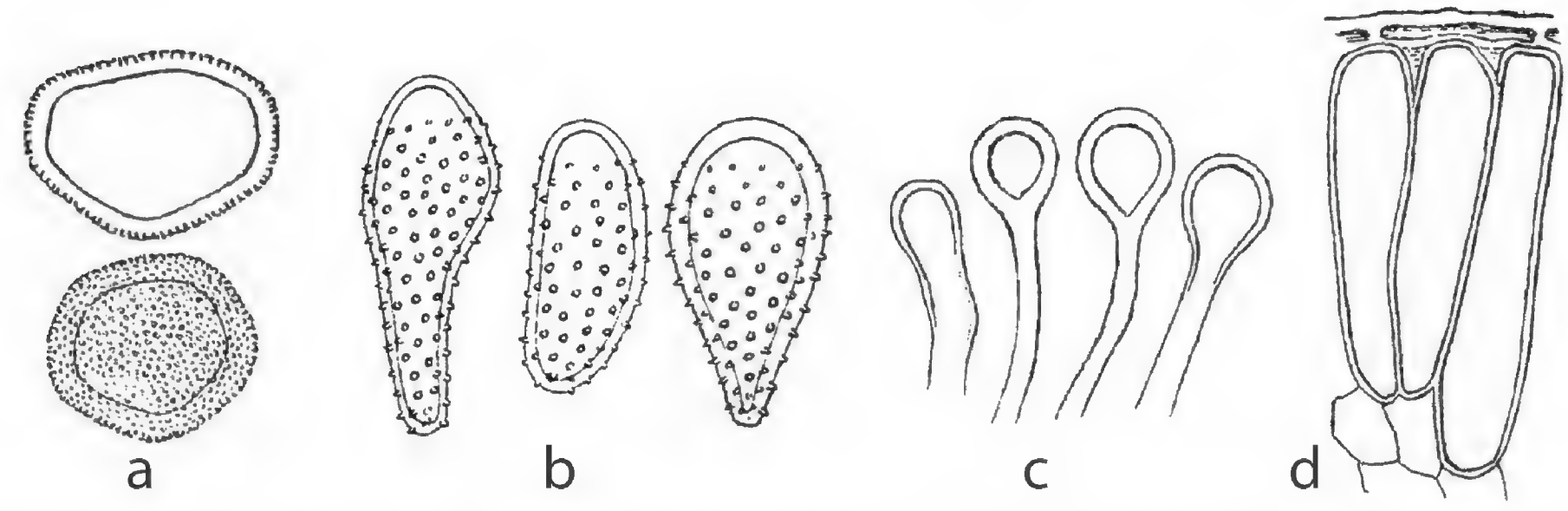


Figure 53. *Melampsora vitellinae*. **a.** On *Allium vineale*: aeciospores; **b–d.** On *Salix alba*: **b.** Urediniospores with smooth apex; **c.** Paraphyses with rather thin walls; **d.** Subepidermal teliospores; (**a–d** from Klebahn 1914: 782, as *M. allii-salicis-albae*).

alpine zone. In the Alps, upwind may transport urediniospores from sites of *Salix alba* to sites of *S. retusa*. In Switzerland, *S. retusa* is more frequently infected by *M. laricis-epitea* than by *M. vitellinae* (Gäumann 1959). – For the distribution of *M. vitellinae* in Austria see Poelt and Zwetko (1997: 84, as *M. salicis-albae*).

Key to the *Melampsora* species on *Salix retusa*

1a Urediniospores elongate; wall echinulate at sides, but smooth at apex ..... *M. vitellinae*
1b Urediniospores (broadly) ellipsoid; wall evenly echinulate ..... (*M. epitea* s.l.) 2
2a Urediniospores rather large (17–35 × 15–23 µm). Uredinial paraphyses rather long (60–95 µm); head 18–41 µm wide; wall thickness up to 10 µm ..... (*M. epitea* var. *reticulatae*) *M. reticulatae*
2b Urediniospores smaller. Uredinial paraphyses shorter (35–80 µm), head 15–24 µm wide; wall thickness up to 6 µm ..... (*M. epitea* var. *epitea*) 3
3a Urediniospores 14–20 × 11–16 µm. Wall conspicuously densely echinulate; spine density 0.9 spines/µm²; spine distance (1–)1.4(–2) µm (see also Fig. 28a, p. 216) ..... *M. arctica*
3b Urediniospores 18–22 × 14–18 µm. Wall less densely echinulate, approx. 0.55 spines/µm²; spine distance 2 µm (see also Fig. 28c, p. 216) ..... *M. laricis-epitea*

(37) *Melampsora* sp.

Auteu-form(?):
(0–III on: *Saxifraga aizoides*)

No detailed description is available for spermatogonia, aecia and aeciospores. – **Uredinia** epiphyllous, minute, roundish. Paraphyses (not described by Gäumann 1959) mainly capitate, occasionally clavate, 50–70 µm long; head 15–20 µm wide; wall thickness even, 2–3 µm. – **Urediniospores** ellipsoid, 16–20 µm long, 15 µm wide, yellow-orange; wall finely echinulate. – **Telia** minute, densely crowded, chestnut-brown. – **Teliospores** clavoid, 40–50 µm long, 14 µm wide. – Reference: Gäumann (1959: 190).

Remarks. This rust has been found in Ticino (Switzerland). It may represent a distinct species. Majewski (1977) and Urban and Marková (2009) reported that uredinia and telia on *Saxifraga aizoides* have also been found in the Tatra Mountains, but the material is not preserved.

(38) *Melampsora* sp.

Life cycle insufficiently known:
(II,III on: *Salix myrtilloides*)
No description available.

Remarks. This rust is reported by Brandenburger (1994) sub *Melampsora salicina* from Bavaria. Jørstad (1940) emphasised that *M. epitea* var. *reticulatae* is the only rust found in N Norway on *Salix myrtilloides*. The same author (Jørstad 1953) noted that two records of uredinia on *S. myrtilloides* from Finnmark approach typical *M. epitea* (i.e., *M. epitea* var. *epitea*). In Austria, *S. myrtilloides* is a very rare willow species.

(39) *Melampsora* sp.

Syn. ***Caeoma cernuae*** Lindf.

Life cycle insufficiently known:
(0,I on: *Saxifraga cernua*)

Spermatogonia between the aecia, subepidermal, lenticular, reddish-brown. – **Aecia** caeomoid, usually hypophyllous, roundish, yellow, surrounded by numerous clavate paraphyses. – **Aeciospores** 19–22 × 17–22 µm, globoid to broadly ellipsoid, but slightly angular; wall up to 3 µm thick, hyaline, densely and finely verrucose. – Reference: Gäumann (1959: 174–175).

Remarks. This taxon raises questions. Do the clavate hyphae around the sori really represent paraphyses? Aecial paraphyses are lacking in *Melampsora*. Gäumann (1959) placed *Caeoma cernuae* in the 'Formenkreis' of *Melampsora alpina* (now *M. arctica*). However, in inoculation experiments with its aeciospores, Lindfors (1913) got abortive infection on *Salix reticulata* and no infection on *S. lapponum*. *Caeoma cernuae* has been described from N Sweden. Jørstad (1940) noted that it probably belongs to the *M. epitea* complex, as its host is closely allied to *Saxifraga rivularis*. Neither Hylander et al. (1953) nor Gjærum (1974) reported *Caeoma cernuae* from Scandinavia; they listed *Saxifraga cernua* as host of *M. epitea* s.l. Also, Parmelee (1989) assigned caeomoid aecia on this host plant from arctic Canada to *M. epitea* s.l. Gäumann (1959) noted that *M. arctica* produces aecia on *S. cernua*. This rust species is a member of the *M. epitea* complex.

The distribution of the host plant is circumpolar and arctic-alpine; the distribution of the rust is probably circumpolar (Gäumann 1959). Therefore, *Caeoma cernuae* may occur in Austria, but its host is rare in our country (Poelt and Zwetko 1997).

(40) *Melampsora* sp.

Syn. ***Caeoma epilobii-alpini*** Jørst.

Life cycle insufficiently known:
(0,I on: *Epilobium anagallidifolium*?, *E. alsinifolium*, *E. palustre*)

Spermatogonia epiphyllous, scattered, 180 µm in diam., 60 µm high, in bright leaf spots. – **Aecia** caeomoid, hypophyllous, 0.5–1 mm in diam., orange, in yellow to golden spots (2–3 mm in diam.). – **Aeciospores** 15–23 × 14–20 µm, globoid to ellipsoid, but slightly angular; wall about 1 µm thick, densely and finely verrucose. – References: Gäumann (1959: 177), Gjærum (1974: 21).

Remarks. Jørstad (1940) reported that *Caeoma epilobii-alpini* has been found in close vicinity to telia of *Melampsora epitea* type on overwintered leaves of *Salix phylicifolia*, which suggests a connection between the two rust stages. *Caeoma epilobii-alpini* is known from Scandinavia on *Epilobium hornemannii*, from which the type of this rust species was described, but also on *E. alsinifolium*, *E. lactiflorum* and *E. palustre*. Gäumann (1959) listed *E. alpinum*, *E. alsinifolium*, *E. hornemannii*, *E. lactiflorum* and *E. palustre* as hosts. He treats *E. alpinum* L. as a synonym of *E. anagallidifolium* Lam. In contrast, Hoch et al. (1995) reject *E. alpinum* L. as 'nomen ambiguum' because it subsumes the four species *E. alsinifolium* Vill., *E. anagallidifolium* Lam., *E. hornemannii* Rchb., and *E. lactiflorum* Hausskn. Therefore, it is somewhat uncertain if *Caeoma epilobii-alpini* occurs on *E. anagallidifolium*. Poelt and Zwetko (1997) did not record *C. epilobii-alpini* from Austria.

41 *Melampsora* sp.

Syn. ***Caeoma leucoji-verni*** Wróbl.

Life cycle insufficiently known:

0,I on: *Leucojum vernum*

Spermatogonia and **aecia** as in *Melampsora allii-fragilis*. – **Aeciospores** 18–22 × 13–19 µm, globoid to subgloboid; wall hyaline, conspicuously verrucose. – Reference: Gäumann (1959: 162).

Remarks. Gäumann (1959) and Klenke and Scholler (2015) expected that this rust belongs to *Melampsora galanthi-fragilis*. Majewski (1977) listed *Caeoma leucoji-verni* as a synonym of *M. allii-fragilis*, but Laundon (1965b) noted that the aeciospores of *C. leucoji-verni* are slightly smaller when compared to those of *M. allii-fragilis* s.l. – For a record of *Caeoma leucoji-verni* in Austria see Poelt and Zwetko (1997: 84).

(42) *Melampsora* sp.

Syn. ***Caeoma scillae*** Wróbl.

Life cycle insufficiently known:

(0,I on: *Scilla bifolia*)

Spermatogonia epiphyllous, in small groups. – **Aecia** caeomoid, hypophyllous, occasionally epiphyllous, in elongate or roundish groups, often confluent, in wide, pale green leaf spots. – **Aeciospores** 19–27 × 17–22 µm, globoid to subgloboid or angular; wall thin, hyaline, densely verrucose; warts circular-roundish in cross-section; contents yellowish. – References: Gäumann (1959: 159), Majewski (1977: 345).

Remarks. *Caeoma scillae* has been described from Poland. It is not listed in Poelt and Zwetko (1997) but has already been found in Bavaria. According to Gäumann (1959), it probably pertains to a *Melampsora* on *Salix*.

(43) *Melampsora* sp. (*Caeoma* sp.)

Life cycle insufficiently known:

(0,I on: *Allium schoenoprasum*)

Spermatogonia in bright leaf spots. – **Aecia** caeomoid, roundish or elongate, yellow-orange. – **Aeciospores** 18–21 × 16–20 µm, globoid to ellipsoid, sometimes slightly angular; wall about 2 µm thick, densely verrucose; warts about 1 µm high. – Reference: Gjærum (1974: 22).

Remarks. Gjærum (1974) reported this unnamed *Caeoma* on *Allium sibiricum* from N Norway. Friesen (1996) showed *A. sibiricum* to be a synonym of *A. schoenoprasum*. Since this host occurs in our area, this *Caeoma* may be found in Austria as well. It probably belongs to the life cycle of a *Melampsora* species on *Salix*.

(44) *Melampsora* sp. (*Caeoma* sp.)

Life cycle insufficiently known:

(0,I on: *Allium angulosum*)

No diagnosis available.

Remarks. Because of negative results in inoculation experiments with *Melampsora allii-fragilis* and *M. vitellinae*, Gäumann (1959) did not list *Allium angulosum* as host of *Caeoma*. Majewski (1977) and Braun (1982) reported collections on *A. angulosum* from Poland and Germany, respectively, which they assigned to *Caeoma allii-ursini*. The latter taxon is often used as a box for all not clearly assignable caeomoid aecia on *Allium* species.

45 *Melampsora* sp. (*Caeoma* sp.)

Life cycle insufficiently known:

0,I on: *Allium scorodoprasum*

Spermatogonia surrounded by aecia, pulvinate. – **Aecia** caeomoid, on both sides of the leaf, surrounded by the ruptured epidermis. – **Aeciospores** subgloboid to ellipsoid or ovoid to more elongate, often ± angular, (17–)22–30(–35) × (14–)17–25 µm; wall 2–2.5 µm thick (often with thicker areas up to 4 µm?), hyaline, verrucose.

Remarks. Poelt and Zwetko (1997: 87) have assigned the two Austrian collections on *Allium scorodoprasum* to *Caeoma* cf. *allii-ursini*. Because of negative results in inoculation experiments with *Melampsora allii-fragilis* and *M. vitellinae* (*M. salicis-albae*) Gäumann (1959) did not list *A. scorodoprasum* as host of *Caeoma*. The aeciospores

from *A. scorodoprasum* are apparently very similar to those of *M. allii-fragilis*, *M. vitellinae* and *M. allii-populina*, but slightly larger and with slightly thicker walls.

46 *Melampsora* sp. (*Caeoma* sp.)

Fig. 54a

Life cycle insufficiently known:

I on: *Hypericum calycinum*

Spermatogonia and telia not observed; uredinia presumably lacking. – **Aecia** caeomoid, hypophyllous, producing bright then brownish spots on the upper side of the leaf. – **Aeciospores** 21–25 × 16–21 µm; wall 2–2.5 µm thick with thinner areas (germ pores?), hyaline, verrucose; warts often irregularly elongated. – Reference: Poelt and Zwetko (1991: 68–69).

Remarks. This rust on cultivated *Hypericum calycinum* is only known in its aecial stage and has frequently been found since 1989; it reduces the commercial value of its host plant considerably. Poelt and Zwetko (1991, 1997) have assigned it to *Melampsora hypericorum*, although not without reservation. The rust on *H. calycinum* has distinctly larger aeciospores with thicker walls and coarser wall ornaments than Austrian collections of *M. hypericorum*. The latter species (probably an autopsis-form, see above) is known to occur on wild species of *Hypericum* in Austria, but the rust on cultivated *H. calycinum* is obviously introduced. For the time being, the taxonomic status of this neomycete remains uncertain; for instance, aeciospore walls of *M. hypericorum* found on two Mediterranean *Hypericum* species (*H. androsaemum* and *H. hircinum*) are as thick as those on *H. calycinum*. – For records of this rust on *Hypericum calycinum* in Austria see Poelt and Zwetko (1991; 1997: 79, under *M. hypericorum*).

47 *Melampsora* sp.

Fig. 55

Syn. ***Uredo hyperici-humifusi*** Kleb.

Life cycle insufficiently known:

II on: *Hypericum humifusum*

Spermatogonia, aecia and telia unknown. – **Uredinia** hypophyllous, up to 0.5 mm in diam., pulvinate, orange, surrounded by the ruptured epidermis; producing pale spots on the upper side of the leaf. Spore mass intermixed with paraphyses. Paraphyses capitate, 50–60 µm long; head 18–22 µm wide; wall 3.5 µm thick, smooth, hyaline. – **Urediniospores** borne singly on pedicels, 18–21 × 14–16 µm, often somewhat polyhedral; wall about

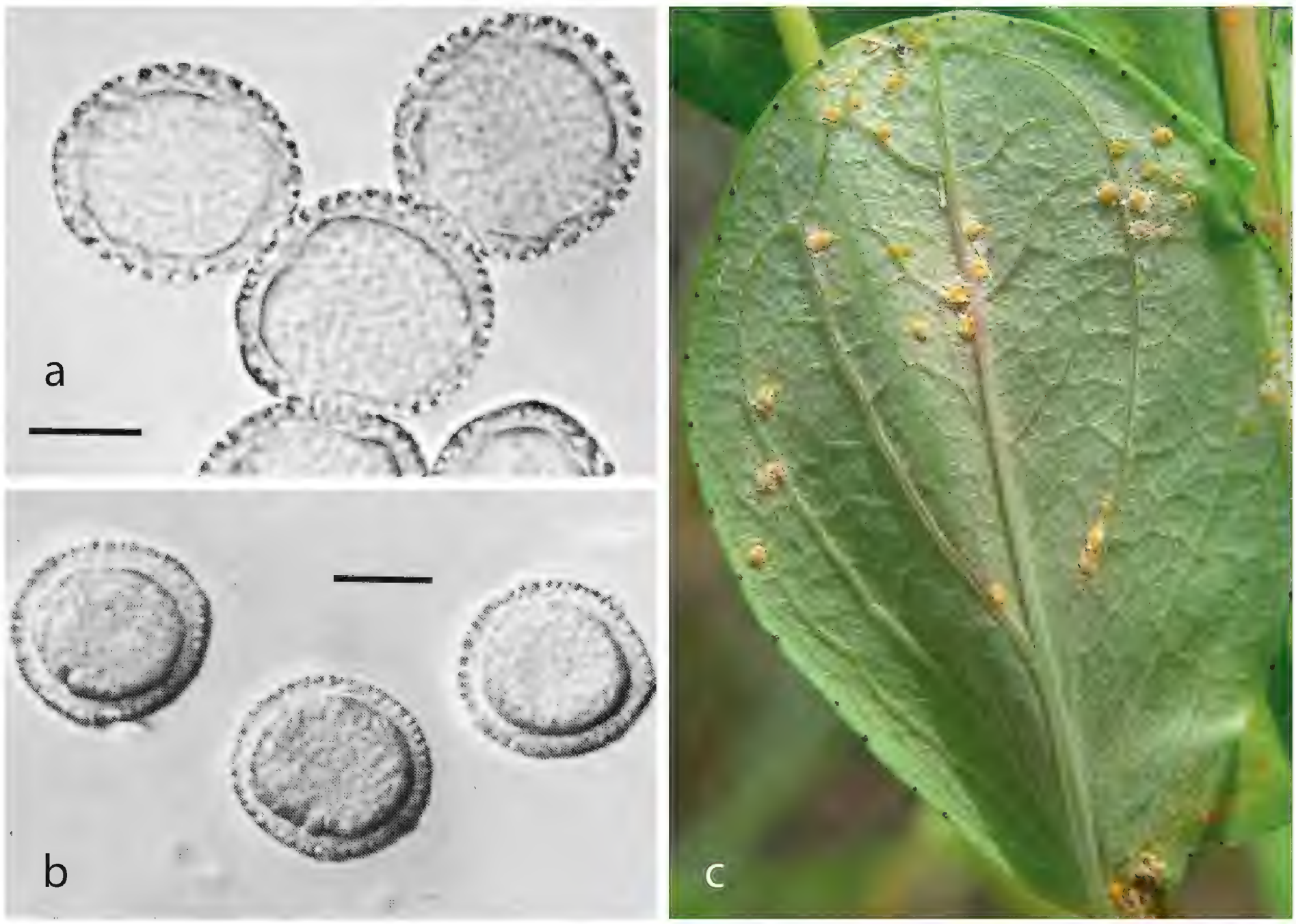


Figure 54. *Melampsora* on *Hypericum*. **a.** *Melampsora* sp. (*Caeoma* sp.) on *Hypericum calycinum*, aeciospores; **b, c.** *Melampsora hypericorum* on *Hypericum montanum*; **b.** Aeciospores; **c.** Aecia. *M. hypericorum* has smaller aeciospores (16–19 × 13–17 µm) with thinner walls and finer warts. Scale bar: 10 µm; (**a, b** from Poelt and Zwetko 1991: 68; **c** by Julia Kruse).

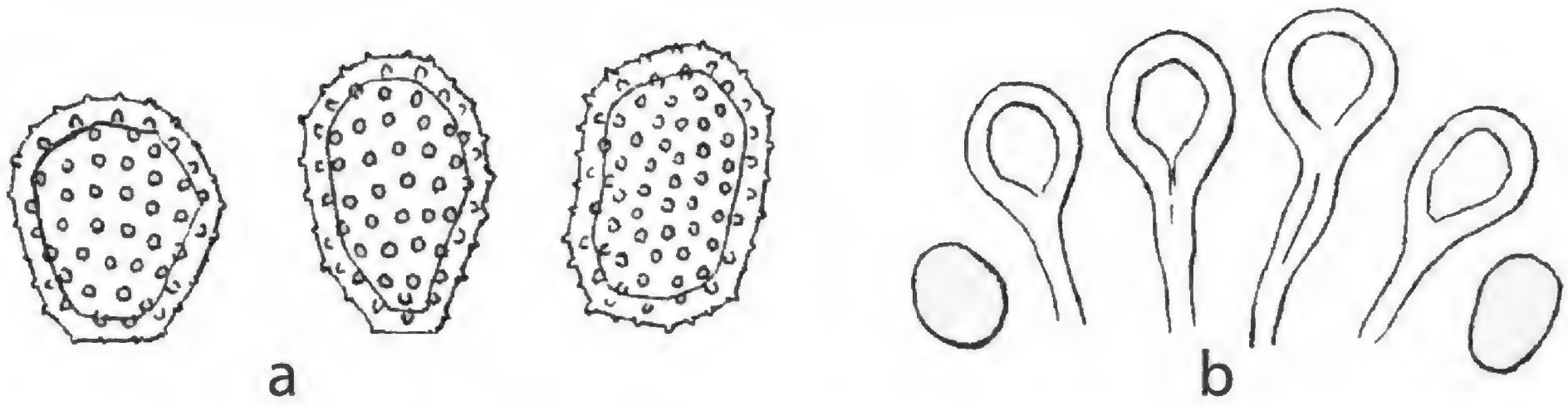


Figure 55. *Melampsora* sp. (*Uredo hyperici-humifusi*) on *Hypericum humifusum*: **a.** Urediniospores; **b.** Paraphyses with spores on the same scale; (**a, b** from Klebahn 1914: 812).

2 µm thick, echinulate-verrucose; distance of warts about 2 µm. – Reference: Gäumann (1959: 187–188).

Remarks. Due to the morphology of the uredinia, this anamorphic taxon corresponds with the genus *Melampsora*. According to Klebahn (1914), its uredinia look like the aecia of *Melampsora hypericorum*. Examination by light microscopy is necessary to distinguish these two taxa. – For records of this rust in Austria see Poelt and Zwetko (1997: 85).

Milesinaceae Aime & McTaggart

The following diagnosis and description are cited from Aime and McTaggart (2020: 32): "Diagnosis: Similar to other Melampsorineae, differing in either production of colourless urediniospores in species that infect ferns, or in production of milesia-type aecia in species that infect Ericaceae." … "Description: With typically colourless sori, although urediniospores of *Naohidemyces* are orange, otherwise similar to Pucciniastraceae. Spermogonia Group I (mostly type 1, also type 2 and 3); aecia peridermium-type, milesia-type [primary uredinia] in *Naohidemyces*; uredinia milesia-type. Teliospores with dormant germination, 1- to many-celled, barely differentiated, sometimes laterally adherent, typically formed within host epidermal cells. Most species macrocyclic and heteroecious with sporothalli on ferns (excepting *Naohidemyces* on Ericaceae), and gametothalli on Pinaceae [*Abies* and *Tsuga*]."

Milesina Magnus

Syn. *Milesia* F.B. White s. Gäumann (1959)

As long as *Milesina* species do not outlast as mycelium or urediniospores, they alternate between their hosts *Abies* (aecial host) and various ferns (uredinial and telial hosts). According to this, they are bound to a rather direct contact between fir and ferns. They can be found mainly in humid forests, predominantly in ravines of the montane level of the mountains. Records from Austria usually refer to the uredinial stage. Aecia can be assigned to a particular *Milesina* species only when found in close vicinity to infected ferns, i.e. by unambiguous field observation, by inoculation experiments, or by molecular genetic evidence.

In *Milesina* only aecia and uredinia are visible to the naked eye; teliospores can hardly be detected even by light microscopy. – **Spermatogonia** hemispherical, hyaline, subepidermal or subcuticular (according to Gäumann 1959; Wilson and Henderson 1966; Majewski 1977); subepidermal (according to Cummins and Hiratsuka 1983, 2003). – **Aecia** peridermioid, hypophyllous, subepidermal in origin, erumpent; peridium white, cylindrical, when mature rupturing at the apex; spore mass white. – **Aeciospores** catenulate; wall hyaline, closely and finely verrucose (warts annulate in SEM), or with short irregularly disposed papillate ridges; contents hyaline. – **Uredinia** subepidermal, pustular or immersed, with a hemispherical or flat peridium, opening by an irregular pore without clearly differentiated ostiolar cells; spore mass white. – **Urediniospores** borne singly on short pedicels, globoid, ellipsoid or obovoid; wall hyaline, mostly echinulate, but sometimes inconspicuously verrucose or smooth; contents hyaline. – **Telia** indefinite. – **Teliospores** unstalked, mostly 2- or more-celled by vertical septa, formed within the epidermis cells of the host plant, one or few in each cell, but by repeated septation nearly or quite filling the cell; wall thin, hyaline, smooth, with 1 germ pore in the outer wall of each cell. – Often, the telia are developing in overwintered fronds in spring and germinate without dormancy, but telia of *M. kriegeriana* have also been found in autumn.

Despite the morphological homogeneity of the genus, some of the morphological characters have been described contradictorily. Using light microscopy, Cummins (1936) found germ pores in many species. Henderson and Prentice (1977) have found no evidence of germ pore formation in the walls of urediniospores of *Milesina blechni*. Possibly the TEM pictures by Berndt (1993) show germ pores of *M. blechni* shortly before germination and, therefore, more conspicuously developed. In their diagnosis of the genus, Cummins and Hiratsuka (1983, 2003) stated 'pores bizonate, obscure'. Also, the position of the spermatogonia has been controversially discussed (see above).

The history of the nomenclatural conflict between *Milesia* and *Milesina* under the provisions of the ICBN/ICN is at least quite illustrative. We comply with recent recommendations (e.g., Aime et al. 2018b) and give *Milesina* Magnus (1909) priority over *Milesia* F.B. White (1878) – although not without reservation. At first, *Milesia* has only been based on the description of the anamorph (uredinia). Faull (1932) found teliospores in White's type material of *Milesia polypodii* F.B. White (1878) on *Polypodium vulgare* and chose accordingly the generic name *Milesia* F.B. White instead of *Milesina* Magnus. He noted that the type species *Milesia polypodii* is conspecific with *Melampsorella dieteliana* Syd. & P. Syd. (Sydow and Sydow 1903) which had been based on the description of both spore states, urediniospores (anamorph) and teliospores (teleomorph). Faull also proposed that the Code should be amended in order to extend recognition to uredinial characters as a criterion of priority. In *Milesina*, teleomorphic characteristics are of only minimal taxonomic value in species delimitation. In contrast, the urediniospores exhibit distinctive morphological characters for discrimination of species. The Code accepted at that time caused particular problems in *Milesina* where many species were described and named only on the basis of the uredinial states. "Characters derived from the urediniospores have been the deciding factors for both genus and species in all instances up to the present time, though the teliospores have supplied confirmatory characters as to the genus" (Arthur and Cummins 1962: 6). Gäumann (1959) expressed a different opinion about the validity of the generic name *Milesia*. He emphasised that Arthur (1906) had already validated the name *Milesia* F.B. White by amending the description, i.e., by including the teleomorph. He created a new taxon 'Tribus II, Milesieae nom. nov.' with the following description: "Teliosporen solitär" (Arthur 1906: 337). This tribus only includes one genus, *Milesia*. Therefore, the name *Milesina* Magnus (1909) is superfluous. *Milesia* F.B. White is considered to be a natural genus based on the teleomorph by Faull (1932), Jørstad and Nannfeldt (1958), Gäumann (1959), Arthur and Cummins (1962), and Poelt (1985). Other authors supposed that the teliospores in the type material of *Milesia* were not known when Arthur wrote his paper, and that the description of telia in Arthur's paper possibly refers to another material which he did not specify. They also rejected Faull's interpretation of the Code and his proposition to amend the Code. By Cummins and Hiratsuka (1983, 2003), Brandenburger (1985) and Ono et al. (1992), *Milesia* F.B. White is considered to be the anamorph of the teleomorphic genus *Milesina* Magnus. We would like to draw attention to another view of the nomenclatural situation of the genus *Milesia*: It was Arthur's practice to give nomenclatural priority to the earliest published name irrespective of whether it was based on anamorph (uredinium) or teleomorph (telium). His point of view is now in agreement with article 59 of the current Code (ICN 2012, 2018).

Aime et al. (2018b) also recommended protecting the name *Milesina* Magnus over *Milesia* F.B. White. Two years later, however, Aime and McTaggart (2020: 32–33) wrote: "... our data show that the type of *Milesina*, *M. kriegeriana* (Magnus) Magnus, is not congeneric with the type of *Milesia*, *M. polypodii* F.B. White (fig. 2), thus we recommend retaining both genera at this time. Should future work demonstrate that *Uredinopsis* is polyphyletic, then disposition of these taxa will need revision."

For the time being, we prefer to treat *Milesia* F.B. White as a synonym of *Milesina* Magnus, also because of the involvement of the name *Milesia* in morphological terminology. Cummins and Hiratsuka (2003) and their followers use the name *Milesia* for a broadly defined type of uredinia ('milesia-type'), including those of *Milesina*, *Cronartium*, *Hyalopsora*, *Melampsorella*, *Melampsoridium*, *Naohidemyces*, *Pucciniastrum*, *Thekopsora*, and *Uredinopsis*. In our opinion, the uredinia of these genera are not uniform and should not be united in this manner, although they all pertain to the Melampsorineae. Finally, it must be noted here that Ono et al. (1992) proposed to use the name *Milesia* for the anamorphs of *Phakopsora* and *Cerotelium* as well. However, there is no close relationship between *Milesia*/*Milesina* and those two genera: hosts of *Phakopsora* and of the *Cerotelium* species discussed by Ono et al. (l.c.) are legumes, but hosts of *Milesia*/*Milesina* are ferns.

An excellent study on the identification of *Milesina* species based on detailed descriptions of the urediniospores has recently been published by Bubner et al. (2019).

1 *Milesina* sp.

Fig. 56a, b

Life cycle insufficiently known:

0,I on: *Abies alba*, (*A. cephalonica*, *A. concolor*, *A. grandis*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)

Collections of aecia on *Abies* needles can be assigned to a species usually only on the basis of unambiguous observation in the field, infection studies, or molecular genetic evidence. Gäumann (1959) points out that to his knowledge *Milesina vogesiaca* needs the longest time to produce its aecia when compared to all other species. In nature, its aecia cannot be found before late summer. Of the two samples from Styria, the aecia on needles of the current season had been found in September (Poelt and Zwetko 1997). Findings on *Abies* species not native to Europe are reported from NW Europe. Whether wall ornaments of aeciospores are suitable to discriminate *Milesina* species remains an open question.

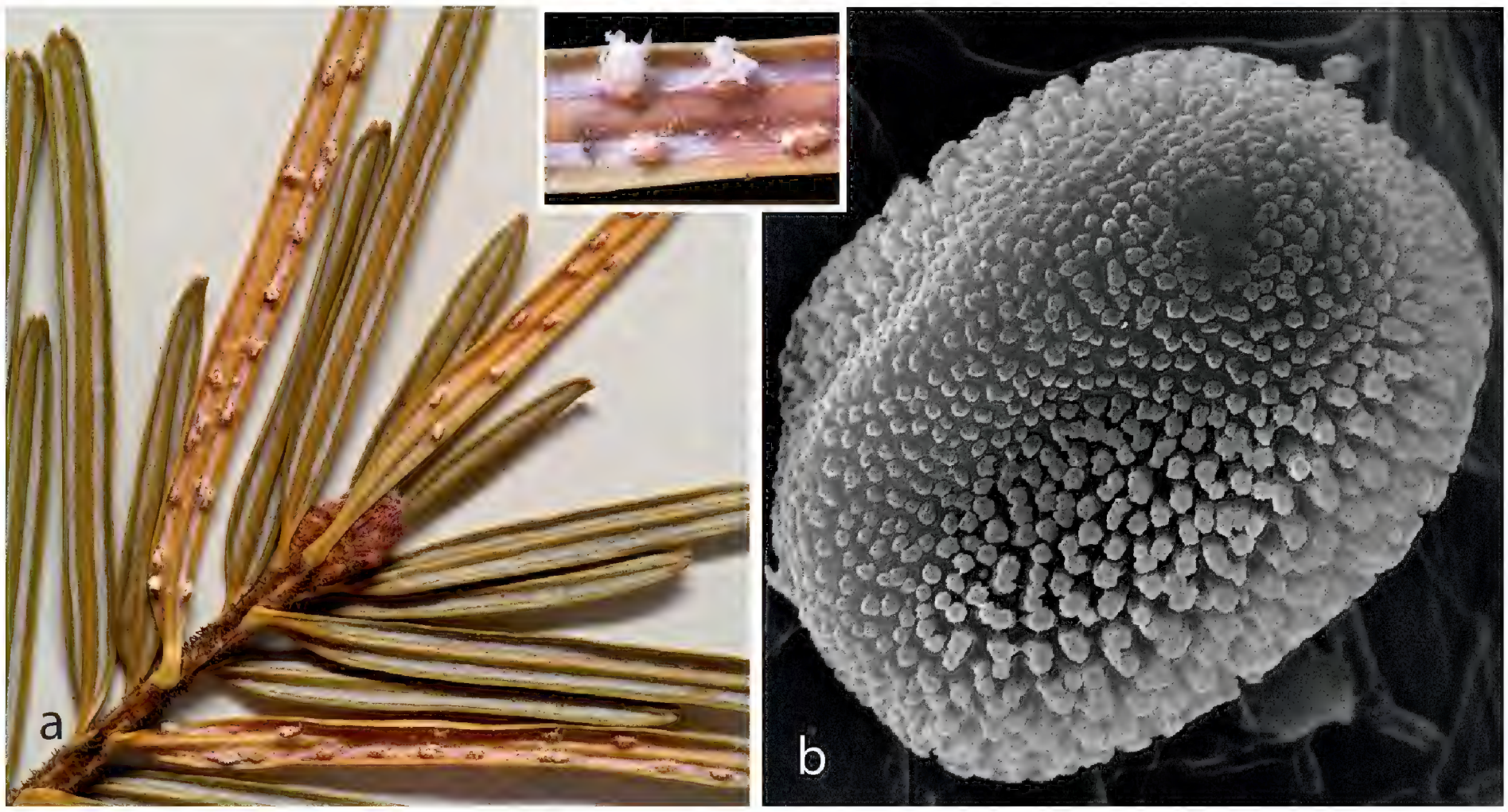


Figure 56. *Milesina*, aecial stage. **a.** *Milesina* sp. on *Abies alba*: aecia hypophyllous, peridia and aeciospore mass white; **b.** *Milesina* cf. *exigua* on *Abies alba*: aeciospore showing the longitudinal zone of small warts from the apex to the base in SEM; (**b** from Zwetko and Blanz 2018: 279).

Key to the rusts on needles of *Abies*

1a Spermatogonia and aecia on yellowish-green needles of witches' brooms ..... *Melampsorella elatina* (syn. *M. caryophyllacearum*)
1b Spermatogonia and aecia on needles, no witches' brooms 2
2a Aecia caeomoid (without peridium). Spore mass bright yellow. ..... *Melampsora abietis-caprearum*
2b Aecia peridermoid (peridium well developed; peridial cells white) 3
3a Spermatogonia on needles of the previous season, aecia on needles of the second previous season; aeciospores pale yellowish to yellow in mass (when fresh) ..... *Hyalopsora aspidiotus*
3b Spermatogonia and aecia on needles of current season; aeciospores yellow to orange in mass (when fresh) 4
3c Spermatogonia and aecia on needles of current season; aeciospores white in mass (even when fresh) 7
4a Aecia only 0.5–0.8 mm high; peridia rupturing longitudinally or irregularly at the apex, at length torn to the base into 3–5 conspicuous segments. Aeciospores 20–40 × 18–29 µm ..... *Pucciniastrum symphyti* (syn. *Melampsorella s.*, *Thekopsora s.*)
4b Aecia mostly 1–2 mm high 5
5a Spermatogonia often lacking. Aeciospores 16–23 × 12–16 µm; wall uniformly thick (about 1 µm), uniformly and finely verrucose ..... *Calyptospora columnaris* (syn. *C. goeppertiana*)
5b Spermatogonia present. Wall of aeciospores not uniformly thick and not uniformly verrucose 6
6a Aeciospores 13–21 × 10–14 µm; wall about 1.5 µm thick and minutely verrucose for the most part, often with a smooth spot where the wall is thinner (1 µm) ..... *Pucciniastrum epilobii*, *P. pustulatum*
6b Aeciospores 14–32 × 11–21 µm; wall up to 2 µm thick and densely verrucose for the most part, often with a smooth strip where the wall is thinner ..... *Pucciniastrum circaeae*
7a Aeciospores 18–24 × 14–22.5 µm (but see the remarks under *M. exigua*!) ..... *Milesina exigua*
7b Aeciospores 18–24 × 15–19 µm ..... *Uredinopsis struthiopteridis*
7c Aeciospores 22–48 × 20–36 µm ..... *Milesina* spp.

2 *Milesina blechni* (Syd. & P. Syd.) Syd. & P. Syd.

Syn. *Milesia blechni* (Syd. & P. Syd.) Arthur

Hetereu-form:
(0,I on: *Abies alba*, *A. cephalonica*)
II,III on: *Struthiopteris spicant* [syn. *Blechnum s.*]

Spermatogonia on needles of current season, amphigenous, but mostly hypophyllous, subepidermal in origin (inner surface of the epidermis appearing ± disorganised), immersed, flask-shaped in section, 110–175 µm in diam., 105–150 µm high. – **Aecia** on needles of current season, hypophyllous, in two rows, erumpent, white, cylindrical, 0.3–0.4 mm in diam., with a delicate,

hyaline peridium; outer wall of peridial cells thin (about 1 µm thick), smooth, inner wall 2.5–3 µm thick, finely and densely verrucose; spore mass white. – **Aeciospores** ellipsoid, ovoid or globoid, 27–36 × 21–27 µm; wall hyaline, thin, densely and rather coarsely verrucose except on one side where the warts are minute (for scanning electron micrographs of the tower-shaped, annulate warts see Berndt 1993: 158). – **Uredinia** hypophyllous, scattered or grouped, in greenish-brown leaf spots of different size, pustular, 0.2–0.4 mm in diam., yellowish, rupturing the overlying epidermis at a centrally placed stoma; peridium hemispherical, hyaline; wall of peridial cells thin, smooth; spore mass white. – **Urediniospores** hyaline, 26–45 × 15–23 µm, mean 33 × 19 µm (after Gäumann 1959), 27.5–42.5 × 15.0–20.0 µm, mostly 30.0–37.5 × 15.0–19.0 µm (after Bubner et al. 2019), ellipsoid to obovoid; wall 0.7–1 µm thick, rather loosely and coarsely echinulate, without spine-free areas; distance between spine bases mostly 1.5–4.0 µm; germ pores scattered, 6–13, mostly 10–11; pedicels c. 12 × 6 µm. – **Telia** hypophyllous, on overwintered fronds, on large, indefinite, brown areas. – **Teliospores** formed within the epidermis cells, also in the guard cells of stomata, 1-celled or divided into many cells by anticlinal septa (up to 70 cells), hyaline, rounded or irregular in shape, often filling the whole epidermis cell; cells of teliospores irregularly polygonal, 8–16 × 6–11 µm; walls thin, smooth, hyaline, with 1 germ pore in the outer wall of each cell. – References: Gäumann (1959: 26–27), Wilson and Henderson (1966: 18–19), Bubner et al. (2019).

Remarks. Bubner et al. (2019) pointed out that urediniospores of *Milesina blechni* are very similar to those of *M. kriegeriana*, only the mean spore length of *M. blechni* is somewhat higher (30.0–37.5 vs. 27.5–35.0 in *M. kriegeriana*).

This rust can persist without host alternation in the uredinial stage. It is widely distributed among the populations of its host. Berndt (1999a) reported that uredinia have not been found on the fertile fronds in SW Germany, but they have been collected frequently on the sterile fronds. – For records of *M. blechni* in Austria see Poelt and Zwetko (1997: 88–89).

3 *Milesina carpatica* Wróbl.

Syn. *Milesia carpatica* (Wróbl.) Faull; *Milesina carpatorum* Hyl., Jørst. & Nannf.

Life cycle insufficiently known:
(0,I on: *Abies alba*?) – Klenke and Scholler (2015)
II,III on: *Dryopteris affinis*, *D. filix-mas* agg., (*Dryopteris carthusiana* agg., *D. filix-mas*)

Spermatogonia and aecia unknown. – **Uredinia** hypophyllous, singly or in groups, in brown leaf spots of different size, pustular, 0.1–0.2 mm in diam., covered by brownish-coloured epidermis ruptured at a central stoma pore; peridium hemispherical, delicate, hyaline; wall of peridial cells thin (0.5–1 µm); spore mass white. – **Urediniospores** hyaline, 14–27 × 11–17 µm, mean 20 × 14 µm (after Gäumann 1959), 16.5–32.5 × 10.0–20.0 µm, mostly 20.0–30.0 × 12.5–19.0 µm (after Bubner et al. 2019), ellipsoid or subgloboid to obovoid; wall 0.5–1(–1.8) µm thick, irregularly echinulate but without spine-free areas; distance between spine bases mostly 0.5–3.0 µm; spines short and delicate; germ pores scattered, 4–10, mostly 5–7; pedicels short. – **Telia** amphigenous, mostly hypophyllous, on overwintered fronds, on indefinite, extensive brown areas. – **Teliospores** formed within the epidermis cells, exceptionally also in the guard cells of stomata, 1-celled or divided into many cells by anticlinal septa (up to 60 cells and more), hyaline, rounded or irregular in shape, often filling the whole epidermis cell; cells of teliospores 8–15 × 5–11 µm; walls thin, smooth, hyaline. – References: Gäumann (1959: 27), Wilson and Henderson (1966: 23), Bubner et al. (2019).

Remarks. The urediniospores of *Milesina carpatica* are distinctly smaller than those of *M. kriegeriana* and their echinulation is more delicate. Both rusts occur on *Dryopteris* spp. – For records of *M. carpatica* in Austria see Poelt and Zwetko (1997: 89, as *M. carpatorum*).

4 *Milesina exigua* Faull

Syn. *Milesia exigua* (Faull) Faull; *Milesina neoexigua* Berndt

Hetereu-form, but spermatogonia and aecia not reported from Europa so far:
(0,I on: *Abies alba*?) – Klenke and Scholler (2015)
II,III on: *Polystichum braunii*, (*P. aculeatum*)

Spermatogonia and aecia not described from Europe so far. – **Uredinia** hypophyllous, scattered or grouped, in yellow-greenish or pale brownish leaf spots, pustular, 0.3 mm in diam., with peridium; spore mass white. – **Urediniospores** hyaline, ellipsoid to obovoid-clavate or irregular in shape, 22.5–30(–32.5) × 12.5–17.5 µm (after Bubner et al. 2019) or greatly fluctuating in shape and size, 20–33.5 × 11.5–15.5 µm (after Poelt 1984); wall about 0.5–0.8(–1?) µm thick, (almost) smooth; germ pores mostly apical, or both basal and apical (bizonate), probably c. 4–6; pedicels short. – **Telia** mostly hypophyllous, on overwintered, brown fronds (or in brown areas, respectively). – **Teliospores** formed within the epidermis cells, but never found in the guard cells of stomata (Poelt 1984), 1- to many-celled (up to 30 cells), with very irregularly inserted anticlinal septa, resembling the epidermis cell in shape; cells of teliospores 9–24 × 9–20 µm; walls thin, smooth, hyaline. – References: Majewski (1977: 67–68), Poelt (1984: 252–254), Bubner et al. (2019: 17–18).

Remarks. Aecia of a '***Milesina* cf. *exigua***' on *Abies alba* have been found in Styria (Scheuer 2004, Mycotheca Graecensis no. 376, as *Milesina* sp.), in close vicinity to uredinia of *M. exigua* on *Polystichum braunii* and of *M. polypodii* (*M. dieteliana*) on *Polypodium vulgare*. The aeciospores in this material (Fig. 56b) measure 25–35 × 17.5–22.5 µm (vid. M. Buchheit, Karlsruhe, 2018) and are smaller than those of *M. polypodii* (see below), but larger

than in the diagnosis of *M. exigua* by Hiratsuka (1936), who stated that the aeciospores are distinctly smaller than those of all other *Milesina* species reported on *Abies* from Europe. Diagnosis of the aecial state of *M. exigua* given by Hiratsuka (1936): Spermatogonia 122–177.5 µm in diam., 111–163 µm high. Aecia cylindrical, 250 µm in diam., 500 µm high, with peridium. Aeciospores 18–24 × 14–22.5 µm; wall 1.5–2.5 µm thick. – For two Austrian records of *Milesina exigua* on *Polystichum braunii* see Poelt and Zwetko (1997: 89).

5 *Milesina feurichii* (Magnus) Grove

Syn. *Milesia feurichii* (Magnus) Faull

Life cycle insufficiently known:
(0,I on: *Abies alba*?) – Klenke and Scholler (2015)
II,III on: *Asplenium septentrionale*, (*A.* ×*alternifolium*)

Spermatogonia and aecia unknown. – **Uredinia** petiolicolous and occasionally amphigenous, subepidermal, scattered on greenish or brown areas of indefinite extent sometimes involving entire fronds, pustular, 0.1–0.2 µm wide, on petioles up to 2 mm long, covered by brownish-coloured epidermis which is ruptured at a centrally placed stoma or by a slit; peridium hyaline, typically developed or consisting of loose, partly disconnected cells; wall of peridial cells 0.5–2 µm thick. – **Urediniospores** hyaline, 27.5–42.5 × 17.5–25.0 µm, mostly 30.0–37.5 × 20.0–22.5 µm, obovoid, ellipsoid or subgloboid; wall 0.5–1.0(–1.8) µm thick, echinulate, mostly with 1 smooth area (rarely 2); smooth area typically central, circular to ovoid, mostly 10.0–15.0 × 7.5–10.0 µm; distance between spine bases 1.0–5.0(–9.0) µm; germ pores scattered, 5–11, mostly 6–7; pedicels up to 18 µm long. – **Telia** petiolicolous and amphigenous (but mostly hypophyllous), on overwintered fronds, on brown areas of indefinite extent. – **Teliospores** formed within the epidermis cells, also in the guard cells of stomata, 1–15-celled in the epidermis cells, 1–4-celled in the guard cells, hyaline, rounded, elongated, occasionally resembling the host cells in shape; cells of teliospores 8–27 × 8–19 µm; walls thin, smooth, hyaline; each cell with 1 germ pore. – Reference: Gäumann (1959: 24–25), Bubner et al. (2019).

Remarks. For a record of *Milesina feurichii* in Austria see Poelt and Zwetko (1997: 89).

6 *Milesina kriegeriana* (Magnus) Magnus

Syn. *Milesia kriegeriana* (Magnus) Arthur

Hetereu-form:
(0,I on: *Abies alba*, *A. cephalonica*, *A. concolor*, *A. grandis*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)
II,III on: *Dryopteris affinis*, *D. carthusiana*, *D. carthusiana* agg., *D. filix-mas*, *D. filix-mas* agg., (*D. borreri* [*D. affinis* agg.], *D. dilatata*)

Spermatogonia on needles of current season, amphigenous mostly epiphyllous, numerous but inconspicuous, irregularly scattered, hyaline, hemispherical in sectional view, subcuticular, 98–168 µm in diam., 94–168 µm high. – **Aecia** on needles of current season, hypophyllous, in two irregular rows, on slightly yellowish areas of the needles; erumpent, cylindrical, 0.3–0.8 mm in diam., 0.5–1.3 mm high; peridium delicate, hyaline, rupturing at the apex; outer wall of peridial cells thin, smooth, inner wall with fine, elevated ridges; spore mass white. – **Aeciospores** ellipsoid, ovoid to globoid, 22–48 × 20–36 µm; wall hyaline, thin (about 1 µm thick), finely verrucose. – **Uredinia** hypophyllous, subepidermal, numerous, scattered or loosely grouped, in greenish to brown leaf spots of indefinite extent, pustular, 0.1–0.3 mm in diam., covered by brownish, discoloured epidermis with a centrally placed stoma; peridium hemispherical, delicate, hyaline; wall of peridial cells thin (about 1 µm thick), hyaline, smooth; spore mass white. – **Urediniospores** hyaline, 25.0–47.5 × 12.5–25.0 µm, mostly 27.5–37.5 × 15.0–20.0 µm, obovoid to ellipsoid; wall 0.5–1.2 µm, mostly 0.8–1.0 µm thick, echinulate, without spine-free areas; distance between spine bases mostly 1.0–4.0 µm; germ pores scattered, 6–14, mostly 10–11; pedicels 2–8 µm long. – **Telia** hypophyllous on fronds, on brown areas of indefinite extent. – **Teliospores** formed within the epidermis cells, occasionally within the guard cells of stomata, 1- to many-celled (up to 40 cells), with anticlinal septa, hyaline, rounded or resembling the epidermis cell in shape, often filling the whole cell; cells of teliospores 8–20 × 6–16 µm; walls thin, smooth, hyaline. – References: Gäumann (1959: 28), Wilson and Henderson (1966: 21), Bubner et al. (2019).

Remarks. According to Wilson and Henderson (1966), telia are formed on fronds of the current season. In Great Britain, they have been found from autumn to spring. Findings of telia in fall are rather uncommon for fern-inhabiting *Milesina* species. Poelt (1984) points out that nearly all *Milesina* species parasitise on ferns with overwintering green leaves. *Milesina kriegeriana* and *M. carpatica* seem to be exceptions from the rule and usually grow on the deciduous ferns *Dryopteris filix-mas*, *D. affinis* agg., and *D. carthusiana* agg.; further studies are needed to describe reliably the life cycles of these two rusts. In Austria, *M. kriegeriana* has not been reported on *Dryopteris dilatata*, but in SW Germany this rust-host combination was found frequently (Berndt 1999a). – For records of *M. kriegeriana* in Austria see Poelt and Zwetko (1997: 89).

(7) *Milesina magnusiana* Jaap

Syn. *Milesia magnusiana* (Jaap) Faull

Life cycle insufficiently known:
(II on: *Asplenium adiantum-nigrum*)

Spermatogonia, aecia and telia unknown. – **Uredinia** hypophyllous, scattered or grouped, in greenish-brown leaf spots of different size, pustular, 0.1–0.4 mm in diam., covered by yellowing epidermis which ruptures at a central

stoma pore; peridium hemispherical, hyaline, delicate; wall of peridial cells thin (less than 1 µm). – **Urediniospores** hyaline, 28–47 × 17–28 µm, mean 35 × 20 µm (after Gäumann 1959), 21.3–38.8 × 15.0–22.5 µm, mostly 30.0–35.0 × 17.5–20.0 µm (after Bubner et al. 2019), ellipsoid to obovoid, rarely globoid or clavoid; wall 0.5–1.2 µm thick (after Gäumann 1959), 1.0–2.0 µm, mostly 1.0–1.5 µm thick (after Bubner et al. 2019), echinulate, mostly with 1 smooth area (rarely 2); smooth area typically central, mostly 15.0–17.5 × 7.5–10.0 µm; spines scattered regularly or irregularly; distance between spines 0.5–9.0 µm, mostly 3.0–5.5 µm; germ pores scattered, 4–9, mostly 5–6; pedicels short. – References: Gäumann (1959: 25), Henderson and Bennell (1979: 476), Bubner et al. (2019).

Remarks. This rust for which teliospores have not been confirmed (Gäumann 1959) is not mentioned by Poelt and Zwetko (1997). Described from Corsica, it has been found in Ireland as well (Henderson and Bennell 1979).

8 *Milesina murariae* (Magnus) Grove

Syn. *Milesia murariae* (Magnus) Faull; *Milesina murariae* (Magnus) Syd.

Life cycle insufficiently known:

(0,I on: *Abies alba*?) – Klenke and Scholler (2015)

II,III on *Asplenium ruta-muraria*

Spermatogonia and aecia unknown. – **Uredinia** hypophyllous and petiolicolous, subepidermal, scattered or loosely grouped, in greenish or yellowish-brown leaf spots of indefinite extent, pustular, small, 0.1–0.2 mm in diam., on petioles up to 3 mm long, covered by pale brownish-coloured epidermis which is ruptured at a centrally placed stoma pore or by a slit; peridium hemispherical, hyaline; wall of peridial cells 1.5–2 µm thick, smooth. – **Urediniospores** hyaline, 25.0–42.5 × 15.0–22.5 µm, mostly 27.5–35.0 × 17.5–22.5 µm, obovoid, ellipsoid or subgloboid; wall 1.2–2.2(–2.5?) µm, mostly around 2.0 µm thick, strongly and rather sparsely echinulate, with mostly 2 ovoidal smooth areas (rarely 1); smooth areas typically central, mostly 12.5–15.0 × 7.5–10.0 µm; spines curved toward base, denser toward both spore poles; distance between spine bases mostly 2.0–3.5 µm; germ pores scattered, 3–9, mostly 5–6; pedicels very short. – **Telia** hypophyllous, on overwintered fronds, on indefinite, extensive brown areas often involving entire fronds. – **Teliospores** formed within the epidermis cells, often also in the guard cells of stomata, 1-celled or divided into many cells by anticlinal septa (up to 15 cells); hyaline, rounded or irregular in shape, often filling the whole epidermis cell; cells of teliospores 10–25 × 7–16 µm; walls thin, smooth, hyaline, with 1 pore in the outer wall of each cell. – References: Gäumann (1959: 24), Wilson and Henderson (1966: 20–21), Bubner et al. (2019).

Remarks. This rather inconspicuous rust causes a yellowish discolouration of the leaves. In SW Germany this species has been found several times on rocks as well as on anthropogenic sites like walls (Berndt 1999a). In Austria, *Milesina murariae* is typical for the ± continental valleys of the inner Alps (Poelt and Zwetko 1997: 89–90).

9 *Milesina polypodii* (F.B. White) Aime & Rossman

Fig. 57

Syn. *Milesia polypodii* F.B. White; *Milesina dieteliana* (Syd. & P. Syd.) Magnus

Hetereu-form:

0,I on: *Abies alba*?, (*A. cephalonica*, *A. concolor*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)

II,III on: *Polypodium interjectum*, *P. vulgare*

Figure 57. *Milesina polypodii* on *Polypodium vulgare* agg.; tiny light-brown uredinia with white tendrils of extruded urediniospores: **a1, a2.** Habit on lower leaf side; **b.** Close-up; (**a** by Julia Kruse).

Spermatogonia on needles of current season, amphigenous, immersed, numerous but inconspicuous, hyaline, plane, hemispherical to slightly flask-shaped in section, subcuticular, 120–228 µm in diam., 105–194 µm high, usually broader than high. – **Aecia** on needles of current season, hypophyllous, in two irregular rows, on slightly yellowish, discoloured areas of the needles, erumpent, white, cylindrical, 0.5–0.7 mm in diam., 1–1.5 mm high; peridium delicate, hyaline, rupturing at the apex; outer wall of peridial cells thin, smooth, inner wall 2.5–3.5 µm thick, with elevated, coarse, short, irregularly orientated ridges; spore mass white. – **Aeciospores** ellipsoid, ovoid or globoid, 28–54 × 20–36 µm; wall hyaline, thin (about 1 µm), on one side densely and rather coarsely verrucose, on the other almost smooth; warts irregular in outline, tapering to a very blunt point, sometimes deciduous. – **Uredinia** hypophyllous, subepidermal, scattered or loosely grouped, in greenish-brown leaf spots of indefinite extent, pustular, 0.1–0.2 mm in diam., covered by a brownish, discoloured epidermis with a centrally placed stoma pore; peridium delicate but firm, hyaline; wall of peridial cells thin (1 µm or less), smooth; spore mass white. – **Urediniospores** hyaline, 26.5–42.5(–48) × 15.0–25.0 µm, mostly 30.0–40.0 × 17.5–22.5 µm, obovoid to ellipsoid, sometimes subgloboid; wall 1–2 µm thick (after Gäumann 1959), 0.5–1.0(–2.5) µm (after Bubner et al. 2019), rather strongly echinulate, with 1 ovoidal smooth area (rarely 2); smooth area typically central, mostly 15.0–17.5 × 7.5–10.0 µm; spines denser toward spore base; distance between spines mostly 1.0–4.0 µm; germ pores scattered, 4–10, mostly 5–6; contents hyaline; pedicels short. – **Telia** hypophyllous, on overwintered fronds, on large, indefinite, brown areas. – **Teliospores** formed within the epidermis cells, occasionally within the guard cells of stomata, 1- to many-celled (up to 50 cells), with anticlinal septa, hyaline, rounded or irregular in shape, often filling the whole epidermis cell; cells of teliospores 12–23 × 8–20 µm; walls thin, smooth, hyaline, with 1 germ pore in the outer wall of each cell. – References: Gäumann (1959: 30–31), Wilson and Henderson (1966: 25–26), Bubner et al. (2019).

Remarks. For records of *Milesina polypodii* in Austria see Poelt and Zwetko (1997: 89, as *M. dieteliana*).

10 *Milesina scolopendrii* (Fuckel) Jaap

Fig. 58

Syn. *Milesia scolopendrii* (Fuckel) Arthur

Hetereu-form:

(0,I on: *Abies alba*, *A. cephalonica*, *A. concolor*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)
II,III on: *Asplenium scolopendrium* [syn. *Phyllitis s.*]

Spermatogonia on needles of current season, amphigenous, numerous but inconspicuous, hyaline,

Figure 58. *Milesina scolopendrii* on *Asplenium scolopendrium*: hundreds of tiny, yellowish-brown uredinia.

hemispherical to slightly flask-shaped in section, subcuticular, 120–228 µm in diam., 100–188 µm high. – **Aecia** hypophyllous on needles of current season, in two irregular rows, white, erumpent, cylindrical, 0.4–0.5 mm in diam., 0.7–1.5 mm high; peridium delicate, hyaline, rupturing at the apex; outer wall of peridial cells smooth, inner wall finely and densely verrucose; warts arranged in elevated, short lines. – **Aeciospores** ellipsoid, ovoid or globoid, mostly elongated, 28–48 × 22–44 µm, white in mass; wall hyaline, thin (about 1 µm thick), very densely and rather coarsely verrucose; warts irregular in outline, tapering to a blunt point, somewhat deciduous. – **Uredinia** hypophyllous, subepidermal, scattered or loosely grouped, frequently in rows between the lateral veins and parallel to them, on greenish to brown areas of indefinite extent, sometimes involving almost the entire frond, pustular, 0.1–0.3 mm in diam., covered by brownish epidermis which is finally ruptured at a centrally placed stoma pore; peridium hemispherical, delicate, hyaline; wall of peridial cells thin (about 1 µm thick), hyaline, smooth. – **Urediniospores** hyaline, 28–57 × 14–23 µm, mean c. 37 × 19 µm (after Gäumann 1959), 27.5–49.0 × 17.5–25.0 µm, mostly 27.5–42.5 × 17.5–22.5 µm (after Bubner et al. 2019), ellipsoid or obovoid to clavate; wall 0.5–1.2(–1.8 µm) thick, quite strongly and rather sparsely echinulate, with 1 usually ovoidal, central to apical smooth area; smooth area mostly 15.0–17.5 × 7.5–10.0 µm; distance between spine bases mostly 2.0–5.0 µm, sometimes denser toward the base; germ pores scattered, 4–9, mostly 6–7; pedicels up to 16 µm long. – **Telia** hypophyllous, occasionally also epiphyllous, on indefinite, brown areas on overwintered fronds. – **Teliospores** formed within the epidermis cells, sometimes also within the guard cells of stomata, 1- to many-celled (up to 40 cells), with anticlinal septa, hyaline, rounded or irregular in outline and conforming to the shape of the containing epidermis cell, often completely filling it; sometimes several 1- to few-celled spores in a single epidermis cell; cells of teliospores 8–25 × 7–15 µm; walls thin, smooth, hyaline, with 1 germ pore. – References: Gäumann (1959:

29–30), Wilson and Henderson (1966: 19–20), Bubner et al. (2019).

Remarks. *Milesina scolopendrii* frequently occurs on the sites of *Asplenium scolopendrium* in SW Germany (Berndt 1999a) and also in Styria. – For records of *M. scolopendrii* in Austria see Poelt and Zwetko (1997: 90).

11 *Milesina vogesiaca* Syd. & P. Syd.

Fig. 59

Syn. *Milesia vogesiaca* (Syd. & P. Syd.) Faull; *Milesina neovogesiaca* Berndt

Hetereu-form:

(0,I on: *Abies alba*, *A. cephalonica*, *A. nordmanniana*, *A. pinsapo*)

II,III on: *Polystichum aculeatum*, *P. lonchitis*, (*P. setiferum*)

Spermatogonia on needles of current season, amphigenous, mostly epiphyllous, numerous but inconspicuous, hyaline, plane, hemispherical to slightly flask-shaped in section, subcuticular, 154–241 µm in diam., 168–214 µm high. – **Aecia** hypophyllous on needles of current season, in two irregular rows, on slightly yellowish discoloured areas, white, erumpent, cylindrical, 0.5–0.7 mm in diam., 0.6–1 mm high; peridium delicate, hyaline, rupturing at the apex; outer wall of peridial cells smooth, inner wall verrucose or with coarse, short, irregularly orientated ridges. – **Aeciospores** ellipsoid, ovoid or globoid, mostly elongated, 32–46 × 24–30 µm, white in mass; wall hyaline, thin (about 1 µm thick), densely verrucose; warts irregular in outline, rather blunt, often deciduous. – **Uredinia** hypophyllous, subepidermal, scattered or loosely grouped on greenish or brown areas of indefinite extent, pustular, round or slightly elongated, 100–300 µm in length, covered by a slightly brownish, discoloured epidermis rupturing at a centrally placed stoma pore; peridium hemispherical, delicate, hyaline; wall of peridial cells 0.5–1.5 µm thick, hyaline; spore mass white. – **Urediniospores** hyaline, 22–40 × 17–22 µm, mean c. 30 × 19 µm (after Gäumann 1959), 27.5–45.0 × 15.0–25.0 µm, mostly 30.0–40.0 × 17.5–20.0 µm, obovoid to ellipsoid, short-stalked; wall 0.5–0.8(–1.0) µm thick, almost smooth or indistinctly verrucose, mainly in the upper part of the spore; verrucae clearly visible with SEM only (e.g., Hafellner and Grill 1982), rather flat or slightly hemispherical, mostly 0.4–0.5 µm in diam.; germ pores 3–8, mostly 5–6, often bizonate, sometimes scattered; pedicels short. – **Telia** hypophyllous, occasionally also epiphyllous, on brown areas of indefinite extent. – **Teliospores** formed within the epidermis cells, sometimes also within the guard cells of stomata, 1- to many-celled (up to 50 cells), with anticlinal septa, hyaline, rounded or irregular in outline and conforming to the shape of the containing epidermis cell, often completely filling it; cells of teliospores 9–17 × 8–14 µm; walls thin, smooth, hyaline, with 1 germ pore. – References: Gäumann (1959: 31–32), Wilson and Henderson (1966: 23–24), Hafellner and Grill (1982: 25–27), Bubner et al. (2019).

Remarks. Three rust species have been reported on fronds of *Polystichum* spp.; two of them, *Milesina exigua* and *M. vogesiaca*, have almost smooth urediniospores. These two species differ slightly in urediniospore dimensions. – For records of *M. vogesiaca* in Austria see Poelt and Zwetko (1997: 90).

Figure 59. *Milesina vogesiaca* on *Polystichum aculeatum*: uredinia extruding white tendrils of urediniospores (photo by Julia Kruse).

12 *Milesina whitei* (Faull) Hirats.f.

Syn. *Milesia whitei* Faull

Life cycle insufficiently known:

(0,I on: *Abies alba*?) – Klenke and Scholler (2015)

II,III on: *Polystichum aculeatum*, *P. setiferum*

Spermatogonia and aecia unknown. – **Uredinia** hypophyllous, subepidermal, scattered or loosely grouped, in greenish or brownish leaf spots of indefinite extent, inconspicuous, pustular, round, 0.1–0.3 mm in diam., covered by a buff, discoloured epidermis which finally ruptures at a central stoma pore; peridium hemispherical, very delicate, hyaline; wall of peridial cells less than 1 µm thick, hyaline; spore mass white. – **Urediniospores** hyaline, 22–40 × 17–22 µm, mean c. 30 × 19 µm (after Gäumann 1959), 27.5–40.0 × 16.5–25.0 µm, mostly 27.5–37.5 × 17.5–22.5 µm (after Bubner et al. 2019), obovoid or ellipsoid to oval, rarely subgloboid; wall 0.5–0.8(–1.0) µm thick, ± strongly and rather sparsely echinulate, without spine-free areas; distance between spine bases 1.0–8.0 µm, mostly 1.5–5.0 µm; spines sharply pointed (see the SEM study by Hafellner and Grill 1982); germ pores scattered, 8–15(–17), mostly 9–13; pedicels short. – **Telia** hypophyllous, on overwintered fronds, on indefinite, brown areas, sometimes involving entire fronds. – **Teliospores** formed within the epidermis cells, 1- to many-celled, with anticlinal septa, hyaline, rounded or irregular in outline and conforming to the shape of the containing epidermis cell, often completely filling it; cells of teliospores 8–20 × 6–15 µm; walls thin, smooth,

hyaline. – References: Gäumann (1959: 33), Wilson and Henderson (1966: 24–25), Hafellner and Grill (1982: 28), Bubner et al. (2019).

Remarks. The urediniospores of *Milesina whitei* differ from those of *M. exigua* and *M. vogesiaca* by the presence of sharply pointed spines (Hafellner and Grill 1982). – For records of *M. whitei* in Austria see Poelt and Zwetko (1997: 90).

Naohidemyces S. Sato, Katsuya & Y. Hirats.

The following combined diagnosis is cited from Sato et al. (1993: 47–48) and Cummins and Hiratsuka (2003: 57), with our preferred terms in square brackets: "Spermogonia subcuticular without bounding structure, Group I (type 3); aecia [primary uredinia] *Milesia*-type, subepidermal in origin, with dome-like peridium with conspicuous differentiated ostiolar cells; aeciospores [primary urediniospores] echinulate, borne singly on inconspicuous pedicels; [secondary] uredinia *Milesia*-type, with dome-like peridium with ostiolar cells; [secondary] urediniospores echinulate, borne singly on inconspicuous pedicels; telia scarcely differentiated; teliospores one cell deep, consisting of several laterally adhering cells within epidermal cells of the host, one germ pore per cell located in the center of the cell, wall pigmented; germination occurs after dormancy (overwintering) on dead leaves; basidia external."

1 *Naohidemyces vaccinii* (Jørst.) S. Sato, Katsuya & Y. Hirats.

Fig. 60

Syn. *Pucciniastrum vaccinii* (G. Winter?) Jørst. s.l.; *Thekopsora vaccinii* (Jørst.) Hirats.f.; *Thekopsora vacciniorum* (DC.) P. Karst.; *Pucciniastrum vacciniorum* (Link) Dietel; *Naohidemyces vacciniorum* (J. Schröt.) Spooner [s.l.]; *Pucciniastrum myrtilli* (Schumach.) Arthur; *Thekopsora myrtilli* (Schumach.) L.L.M. Hunter; *Thekopsora myrtillina* P. Karst.

In Europe probably persisting as hemi-form:
(0,IIa on: *Tsuga*)
IIb,III on: *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, (*V. oxycoccos*)

Spermatogonia and primary uredinia (aecia) have not been found on introduced *Tsuga*. – **Secondary uredinia** hypophyllous, scattered or in groups, small, in small leaf spots, long covered by the overarching epidermis, pustular, with a hemispherical peridium, opening with a pore, pale yellow or yellowish-red; ostiolar cells rather thick-walled; spore mass pale yellowish-orange. – **Urediniospores** 17.5–27.5 × 10–19 µm; wall hyaline, 1–2 µm thick, minutely echinulate; contents orange-yellow when fresh. – **Telia** hypophyllous, forming small, brown, indehiscent crusts. – **Teliospores** formed within the epidermis cells, morecelled by anticlinal septa, 20–30 µm long, 18–23 µm wide (in surface view) and 16–22 µm high (in vertical section); wall uniformly 1 µm thick, nearly hyaline or lightly pigmented, with 1 germ pore for each cell positioned centrally at the spore apex. – References: Gäumann (1959: 58, 60), Sato et al. (1993: 49).

Figure 60. *Naohidemyces vaccinii* on *Vaccinium myrtillus*: uredinia (photo by Julia Kruse).

According to Gäumann (1959, under *Thekopsora*), this rust is reported to show two 'biological species' in Europe. '*Thekopsora*' *myrtillina* differs from '*Thekopsora*' *vacciniorum* in size of urediniospores, and in size and colour of uredinia. For the time being, the status of these two taxa is unresolved:

- **'*Thekopsora*' *myrtillina*** P. Karst. s. Gäumann (1959: 58)
  (no combination in *Naohidemyces*)
  Life cycle insufficiently known:
  IIb,III on: *Vaccinium myrtillus*, *V. uliginosum*

Secondary uredinia pale yellow. – Secondary urediniospores (13–)20–24(–30) × (10–)15–19(–27) µm (mean 21–22 × 17–18 µm). – According to Wilson and Henderson (1966: 39), uredinia on *Vaccinium uliginosum* measure 0.2–0.5 mm, while those on *V. myrtillus* are smaller, 0.15–0.25 mm.

- **'*Thekopsora*' *vacciniorum*** (DC.) P. Karst. s. Gäumann (1959: 60)
  ?= *Naohidemyces vacciniorum* (J. Schröt.) Spooner
  Life cycle insufficiently known:
  IIb,III on: *Vaccinium vitis-idaea*, (*V. oxycoccos*)

Secondary uredinia yellowish-brownish-red. – Secondary urediniospores (17–)22–27(–38) × (10–)17–22(–27) µm (mean 24–25 × 19–20 µm). – According to Wilson and Henderson (1966: 39), uredinia on *Vaccinium vitis-idaea* measure 0.2–0.5 mm.

Remarks. *Pucciniastrum vaccinii* (syn. *Thekopsora v.*) was transferred to *Naohidemyces* by Sato et al. (1993), which is supported by the fact that *Naohidemyces* does not cluster with the sampled *Thekopsora* species in the analyses of Maier et al. (2003). *Naohidemyces* also differs from *Thekopsora* (s.str.) in its repeating uredinia and the different location of the germ pore of the teliospores.

Tsuga is reported as host of the primary uredinial state from E Asia and eastern N America. At least in Central Europe, these rusts outlast on their telial host, but teliospores are produced only rarely (Poelt and Zwetko 1997). – For records of *Naohidemyces vaccinii* in Austria see Poelt and Zwetko (1997: 254, as *Thekopsora v.*).

Uredinopsis Magnus

This rust genus alternates between *Abies* (in the aecial stage) and ferns (in the uredinal and telial stages). Three native and one introduced species occur in Europe. *Uredinopsis* is morphologically very similar to *Milesina*. Both genera have similar host ranges, they occur on similar sites, and they lack pigmentation in all spore states. Therefore, a close relationship between these two genera has been proposed. The monophyly of *Uredinopsis* and *Milesina* is strongly supported by molecular data (Maier et al. 2003) and by haustorial ultrastructure (Berndt 1993). Several authors supposed that these fern rusts are the most basal group in the rust fungi (e.g., Arthur, Gäumann, Savile). They thought that the most ancient rusts also have phylogenetically ancient hosts (ferns). Based on a molecular phylogenetic study, Wingfield et al. (2004) estimated the possibility that the temperate fern rusts are not the most basal rust fungi and suggested that the rusts have initially evolved on primitive angiosperms. Also Hiratsuka and Sato (1982) already stated that the life cycle of these fern rusts is complicated and that their spore states are by no means simple or show primitive characteristics, except for their teliospores which are simple in form and are produced inside the host tissues. – **Spermatogonia** subcuticular or subepidermal, subglobose, minute. – **Aecia** peridermioid, subepidermal in origin, erumpent; peridium white, cylindrical, fragile. – **Aeciospores** catenulate, hyaline; wall hyaline, verrucose. – **Uredinia** subepidermal, with an inconspicuous peridium opening by an apical pore; ostiolar cells not clearly differentiated; spore mass white, often extruded as long tendrils. – **Urediniospores** borne singly on very short pedicels, almost sessile, ± lanceolate and apically mucronate, hyaline; wall hyaline, almost smooth or with a few lines of cog-like warts; germ pores near the ends; contents hyaline. – **Amphisporic sori** (amphioid uredinia) partly resembling the uredinia, but appearing later and rupturing later. – **Amphispores** with long pedicels and thick walls occur in some species. They are usually produced late in the season and serve as a resting stage. – **Telia** indefinite. – **Teliospores** intercellular, scattered singly or in irregular groups in the mesophyll, often borne in large numbers on short lateral branches of the mycelium; 1-celled or 2–6-celled by vertical or oblique septa; wall thin, hyaline, smooth; germ pores one in the outer wall of each cell, obscure; germination of teliospores occurs in overwintered fronds.

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

1 *Uredinopsis filicina* (Niessl) Magnus

Fig. 61

Hetereu-form:

(0,I on: *Abies*)

II,II*,III on: *Phegopteris connectilis* [syn. *Thelypteris phegopteris*]

Figure 61. *Uredinopsis filicina* on *Phegopteris connectilis*: uredinia extruding conspicuous long white tendrils of urediniospores (photo by Julia Kruse).

No findings of spermatogonia and aecia have been reported from Europe so far. – **Uredinia** hypophyllous, subepidermal, scattered, in discoloured leaf spots of indefinite extent, pustular, 0.1–0.3 mm in diam., yellowish-brown; peridium convex, delicate, hyaline, rupturing above; wall of peridial cells thin (less than 1 µm); spore mass white. – **Urediniospores** 24–46 × 8–13 µm (mean about 31 × 10 µm), ellipsoid, obovoid or fusoid, with a conical, broad-based mucro about 12 µm long, hyaline; wall very thin (less than 1 µm thick), sometimes thickened at the base, hyaline, smooth except for a few low, scattered hyaline warts (for transmission electron micrographs showing the development of the warts see Berndt 1993: 134); pedicels very short. – **Amphisporic sori** partly resembling the uredinia, but slightly larger (0.1–0.4 mm in diam.) and wall of peridial cells thicker (about 1 µm thick). – **Amphispores** 14–30 × 8–22 µm (mean 21 × 13 µm), obovoid to irregularly polyhedral, without a mucro, hyaline, white in mass; wall 1–1.5 µm thick, hyaline, finely and closely verrucose; pedicels thin, often longer than the spore. – **Telia** amphigenous, mostly hypophyllous, scattered. – **Teliospores** subepidermal, intercellular, scattered or loosely aggregated in a single layer, usually 2-celled, occasionally 1-celled, globoid to ellipsoid, 14–22 µm in diam. (after Gäumann 1959), 18–24 × 15–16 µm (after Wilson and Henderson 1966); walls thin (about 1 µm thick), smooth, hyaline. – References: Gäumann (1959: 15–17), Wilson and Henderson (1966: 16–17).

Remarks. Gäumann (1959) reported that the amphispores of *Uredinopsis filicina* dehisce and germinate after having passed winter. – For records of *U. filicina* in Austria see Poelt and Zwetko (1997: 253–257).

(2) *Uredinopsis pteridis* Dietel & Holw.

Syn. ?*Uredinopsis macrosperma* (Cooke) Magnus

Hetereu-form:

(0,I on: *Abies*)

(II,II*,III on: *Pteridium aquilinum*)

No findings of spermatogonia and aecia have been reported from Europe so far. – **Uredinia** hypophyllous, subepidermal, scattered or in groups, on yellowish-brown areas bordered by veins, pustular. – **Urediniospores** 27–67 × 10–18 µm, with a mucro about 3–8 µm long; wall 1–1.2 µm thick, with two longitudinal bands of short, broad warts, hyaline. – **Amphisporic sori** partly resembling the uredinia. – **Amphispores** 22–45 × 14–27 µm, without a mucro; wall 2–3 µm thick, finely verrucose. – **Telia** amphigenous, on yellowish-brown to brown areas. – **Teliospores** intercellular, often aggregated in a single, subepidermal layer, or singly scattered; 2–6-celled, mostly 4-celled, 18–36 µm in diam.; walls about 1 µm thick, smooth, hyaline. – References: Dietel (1895: 331), Kuprevič and Uljaniščev (1975: 48–49), Majewski (1977: 56).

Remarks. So far, this species is reported from Russia only. Poelt and Zwetko (1997) do not mention it. *Uredinopsis pteridis* is distributed over wide areas of the world together with its uredinial host. The species is very variable with regard to the size of the urediniospores, but this variability does not seem to be related to geographic distribution or host varieties (Faull 1938a, b; Berndt 2008). The urediniospores are generally described as smooth with the exception of two longitudinal bands of warts. In specimens from South Africa examined by Berndt (2008), the spore wall was never smooth between the longitudinal bands. Ziller (1959) studied western tree rusts in N America and stated that the urediniospores of *U. pteridis* may be 'sparsely verrucose-echinulate'. No recent, comprehensive taxonomic study of *U. pteridis* is available. Therefore, Berndt (2008) has treated this rust as one highly variable species. However, Gäumann (1959) noted that *Pteridium aquilinum* is known as host to no less than five species of *Uredinopsis* and expects one or the other of these to be found in or to enter Central Europe.

3 *Uredinopsis struthiopteridis* F.C.M. Störmer [non (Rostr.) Lind]

Fig. 62

Hetereu-form:

(0,I on: *Abies alba*, *A. balsamea*)

II,II*,III on: *Matteuccia struthiopteris*

Spermatogonia on needles of current season, hypophyllous, covered by the cuticula and parts of the outer wall of the epidermis, inconspicuous, hyaline, plane to hemispherical, 71–129 µm in diam., 45–58 µm high, apically opening by a short slit. – **Aecia** on needles of current season, hypophyllous, in two rows, erumpent, white, cylindrical, 0.2–0.3 mm in diam., up to 1 mm high, with a hyaline peridium rupturing at the apex; outer wall of peridial cells thin (1.2–1.3 µm thick), smooth, inner wall 3–3.5 µm thick, densely and rather coarsely verrucose. – **Aeciospores** ellipsoid, ovoid or globoid, 18–24 × 15–19 µm, white in mass; wall hyaline, 1–1.5 µm thick, densely and rather coarsely verrucose. – **Uredinia** hypophyllous, subepidermal, scattered, in angular, discoloured leaf spots or spots of indefinite extent, pustular, 0.1–0.3 mm in diam.; peridium convex, delicate, hyaline; wall of peridial cells about 1 µm thick; spore mass white. – **Urediniospores** 27–54 × 10–17 µm (mean c. 37 × 13 µm), ellipsoid, obovoid or fusoid, with a filamentous mucro about 21 µm long and 6 µm wide, hyaline; wall about 1 µm thick, hyaline, smooth except for two vertical lines of cog-like warts; germ pores 2, near the ends; pedicels very short. – **Amphisporic sori** partly resembling the uredinia; peridium rather firm; wall of peridial cells up to 2.2 µm thick. – **Amphispores** 18–40 × 14–27 µm (mean c. 27 × 18 µm), angular-obovoid to irregularly polyhedral, without a mucro, hyaline, white in mass; wall 1–4 µm thick, hyaline, finely and closely verrucose; pedicels thin and long. – **Telia** amphigenous, mostly hypophyllous,

Figure 62. *Uredinopsis struthiopteridis* on *Matteuccia struthiopteris*: leaf segment with light-brown uredinia (arrow); released urediniospores (arrowhead) white in mass.

scattered. – **Teliospores** subepidermal, intercellular, scattered or loosely aggregated in a single layer, 1–7-celled, mostly 4-celled, globoid to ellipsoid, 16–25 × 14–24 µm; wall about 1 µm thick, smooth, hyaline; 1 pore in each cell. – Reference: Gäumann (1959: 18).

Remarks. Despite the fact that *Abies alba* has been confirmed as host for *Uredinopsis struthiopteridis* in Europe, the latter may live even without host change in this area. We have found amphisporic sori of this rust in the floodplain of the river Mur S of Graz where *Abies alba* does not grow. – For records of *U. struthiopteridis* in Austria see Poelt and Zwetko (1997: 260).

Pucciniastraceae Gäum. ex Leppik emend. Aime & McTaggart

Taxonomic status and monophyly of this family are far from settled, but some important steps towards a more natural circumscription were taken rather recently (Aime et al. 2018a; Aime and McTaggart 2020). For instance, *Thekopsora* was excluded from *Pucciniastrum* and transferred to Coleosporiaceae, *Naohidemyces* to Milesinaceae. Here the family is restricted to *Pucciniastrum*, *Hyalopsora*, *Melampsoridium*, *Calyptospora*, and *Melampsorella*. Aecial hosts are usually *Abies* spp., *Larix* only for *Melampsoridium*. – The following passages are cited from the brief description by Aime and McTaggart (2020: 34): "Similar to Milesinaceae, but most species with cytoplasmic pigmentation, at least within urediniospores. Spermogonia Group I (type 2 or 3). Aecia peridermium-type; uredinia milesia-type. Telia undergo dormancy with external germination; either formed within epidermal cells, or as a subepidermal crust, …. Most species heteroecious, macrocyclic; *Calyptospora* is demicyclic [opsis-form], …"

Calyptospora J.G. Kühn

Until very recently (see Scholler et al. 2022), this genus has been monotypic. Accumulating molecular genetic evidence might lead to a more stable concept of the genus *Pucciniastrum* and to inclusion of *Calyptospora*.

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

1 *Calyptospora columnaris* (Alb. & Schwein.) J.G. Kühn

Fig. 63

Syn. *Thekopsora columnaris* (Alb. & Schwein.) Hirats.; *Calyptospora goeppertiana* J.G. Kühn; *Pucciniastrum goeppertianum* (J.G. Kühn) Kleb.; *Thekopsora goeppertiana* (J.G. Kühn) Hirats.f.

Heteropsis-form:

[0],I on: *Abies alba*, (*A. balsamea*, *A. cephalonica*, *A. concolor*, *A. grandis*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*, *A. veitchii*)

III on: *Vaccinium vitis-idaea*. – Causing conspicuous deformations of the whole shoot.

(III on: *Vaccinium myrtillus*) – On this host only sporadically observed.

Spermatogonia often lacking, subcuticular (Group I, type 3), hypophyllous, subcuticular, 40–140 µm wide, 13–30 µm high, inconspicuous. – **Aecia** peridermioid, on needles of current season, hypophyllous, usually in two longitudinal rows, on yellowish spots, subepidermal in origin, erumpent, cylindrical or sac-like, with a firm, hyaline peridium, up to 2 mm high, with torn or slit margin; peridial cells irregularly polygonal, thin-walled, minutely verrucose on the inner walls; spore mass orange. – **Aeciospores** globose, subglobose to broadly ellipsoidal, 16–23 × 12–16 µm; wall hyaline, about 1 µm thick, evenly, densely and finely verrucose; contents orange(-red). – **Telia** arising from a systemic mycelium, on elongated and swollen stems, forming a continuous crust, at first clear-pinkish, then reddish-brown. The telia-producing mycelium causes witches' brooms on the affected plants. – **Teliospores** unstalked, formed in the epidermis cells, up to 12 in each cell, densely crowded, ± prismatic by the pressure of the other spores, mainly divided into (2–)4(–5) cells by anticlinal septa, 7–14 µm wide, 16–42 µm high (in vertical section); wall 1(–1.5) thick at sides, up to 3(–5) µm thick at the apex, yellow-brown, smooth, with 1 pore in each cell in the corner where the anticlinal walls meet. – Reference: Gäumann (1959: 65), Cummins and Hiratsuka (2003: 51).

Remarks. In the aecial state on *Abies*, *Calyptospora columnaris* can usually be distinguished from other Pucciniastraceae by the lack of spermatogonia (Blumer 1963). It is also characterised by a specific haustorial ultrastructure (Berndt and Oberwinkler 1995). – For the distribution of *C. columnaris* in Austria see Poelt and Zwetko (1997: 252–253, as *Thekopsora goeppertiana*).

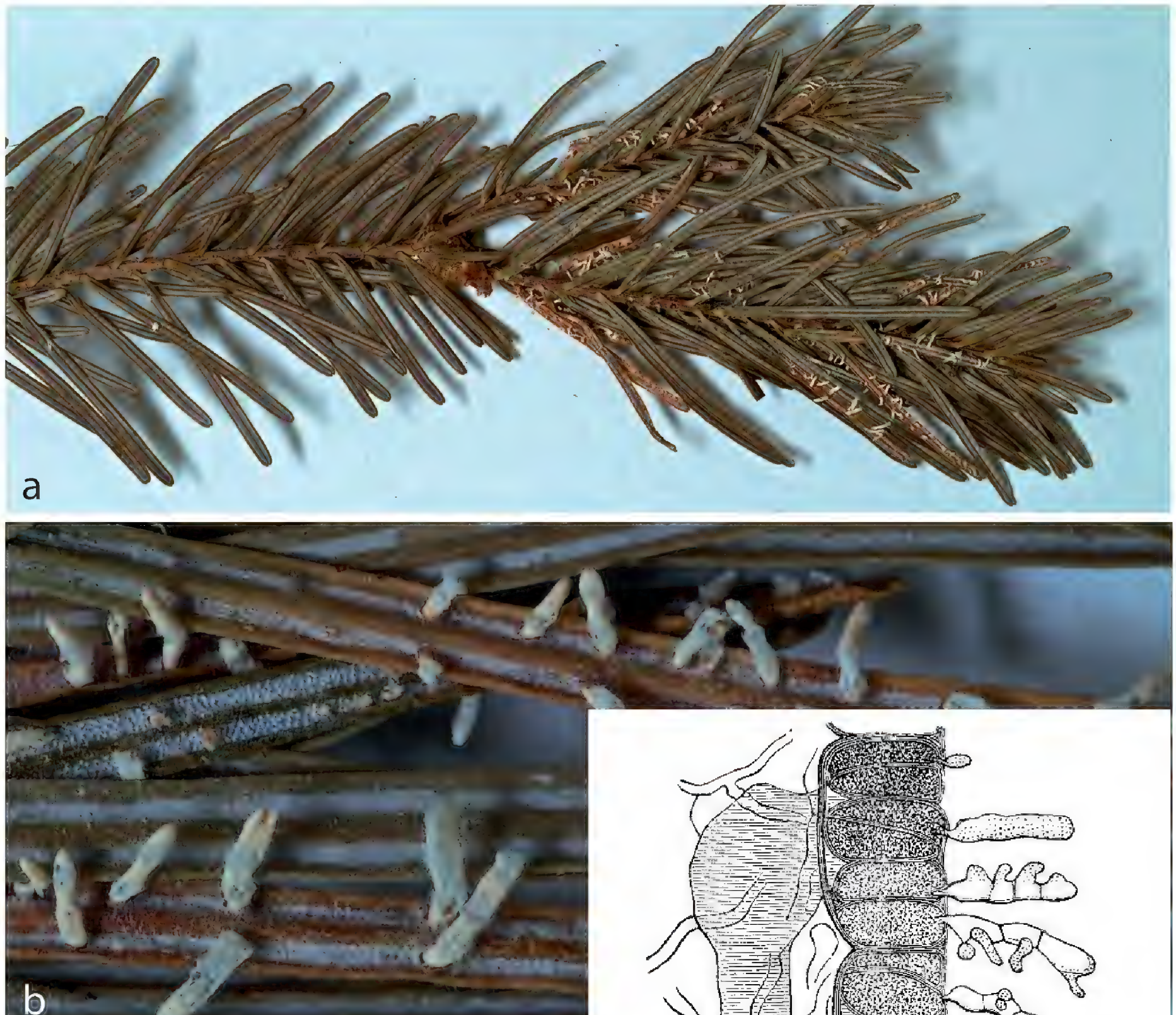


Figure 63. *Calyptospora columnaris*. **a, b.** Aecia on needles of *Abies sibirica*; **c, d.** On *Vaccinium vitis-idaea*: **c.** Infected swollen shoots turning brown with age; **d.** Vertical section through the epidermis with germinated teliospores and 4-celled basidia; (**c** by Julia Kruse; **d** from Dietel 1928: 38, with permission from Duncker & Humblot GmbH).

Hyalopsora Magnus

The species of *Hyalopsora* change from *Abies* in their haplophase to various ferns as does *Milesina*. Macroscopically *Hyalopsora* differs from *Milesina* and *Uredinopsis* in the yellowish to orange colour of its aeciospores and urediniospores. Spore walls are hyaline but carotenoid pigments are present in the cytoplasm (Zwetko and Pfeifhofer 1991). Urediniospores of two kinds exist: thin-walled spores immediately germinating for propagation in summer, and so-called amphispores. Urediniospores of the second kind have thick walls and are produced later in the season; probably they undergo a resting stage before germination and serve for persistence. Telia have only rarely been observed in Austria, while neither spermatogonia nor aecia have been reported at all. When compared with N America or E Asia, the number of *Hyalopsora* species in Europe appears to be very low. In Central Europe, only two species have been found including the type species *H. aspidiotus*. *Hyalopsora adianti-capilli-veneris* occurs in N Italy (e.g., Jaap 1915) and S Switzerland (Berndt and Brodtbeck 2020) on *Adiantum capillus-veneris*. For haustorial ultrastructure of *Hyalopsora*, *Milesina* and *Uredinopsis* see Berndt (1993) and Berndt et al. (1994).

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

Figure 64. *Hyalopsora aspidiotus* on *Gymnocarpium dryopteris*: uredinia.

1 *Hyalopsora aspidiotus* (Peck) Magnus

Fig. 64

Syn. *Hyalopsora polypodii-dryopteridis* (DC.) Sacc.

Hetereu-form:

(0,I on: *Abies alba*, *A. balsamea*)

II,II*,(III) on: *Gymnocarpium dryopteris*, *G. robertianum*

Spermatogonia on needles of the previous season, hypophyllous, subepidermal, usually in two rows on both sides of the midrib, on yellowish spots, covered by yellow-brown epidermis, oval in section, 0.2–0.5 mm in diam., 0.1–0.2 mm high, yellow to orange; without paraphyses. – **Aecia** on yellowish needles of the second previous season, hypophyllous, in two rows on either side of the midrib; subepidermal, erumpent, deeply immersed, bladder-like, spherical, 0.5–0.7 mm in diam., up to 1 mm high (often only 0.2 mm high, after Wilson and Henderson 1966); peridium delicate but persistent, rupturing at the apex, hyaline; outer wall of peridial cells 3–5 µm thick, smooth; inner wall 5–10 µm thick, verrucose; spore mass pale yellowish to yellow when fresh. – **Aeciospores** globoid or broadly ellipsoid, angular, 20–25 × 16–20 µm, yellow; wall hyaline, thin (0.8–1.5 µm thick), densely and finely verrucose. – **Uredinia** subepidermal, amphigenous, but mostly hypophyllous, scattered, often covering the whole leaf surface, usually on yellowish areas; small, round, 0.2–0.5 mm in diam., golden-yellow to orange, at first covered by the epidermis and a thin, delicate peridium, then naked and ± pulverulent. – **Urediniospores** borne singly, pedicellate, ellipsoid to ovoid, 25–36 × 18–25 µm; wall hyaline, thin (1–1.5 µm thick), finely verrucose-echinulate, with 4 indistinct equatorial pores; contents golden-yellow to orange. – **Amphisporic sori** (amphioid uredinia) smaller than the uredinia; mostly indehiscent. – **Amphispores** 40–55 × 27–40 µm, obovoid, ellipsoid or globoid, slightly angular; wall 3–8 µm thick, hyaline, with very faint, hardly perceptible warts, and 6–8 distinct, scattered pores. – **Telia** hypophyllous, on overwintered fronds, on large, yellow areas. – **Teliospores** formed within the epidermis cells, also in the guard cells of stomata, often filling the cells completely, rounded or irregular in shape, flattened where they are in contact, 18–28 µm high, 20–40 µm wide, divided by vertical septa into 2–7 cells; walls thin (1 µm or less), smooth, hyaline; germ pores obscure; germination occurs without dormancy. – References: Gäumann (1959: 34–35), Wilson and Henderson (1966: 27).

Remarks. The uredinia of *Hyalopsora aspidiotus* are produced in summer, and the amphisporic sori usually appear later than the uredinia. Spores intermediate between urediniospores and amphispores occur in some sori. – For records of *H. aspidiotus* in Austria see Poelt and Zwetko (1997: 68).

2 *Hyalopsora polypodii* (Pers.) Magnus

Fig. 65

Life cycle insufficiently known:

II,II*,(III) on: *Cystopteris fragilis*, *C. alpina*, (*Athyrium filix-femina*, *Woodsia pulchella*)

Figure 65. *Hyalopsora polypodii* on *Cystopteris fragilis*: **a.** Discoloured fronds; **b.** Uredinia hypophyllous, orange; (**a, b** by Julia Kruse).

Spermatogonia and aecia unknown. – **Uredinia** subepidermal, amphigenous, mostly hypophyllous, also on petioles, scattered or loosely grouped, often covering the whole leaf surface, usually on indefinite, greenish or brownish areas, very small, 0.2–0.5 mm in diam., pustular, golden-yellow to orange, at first covered by the epidermis and a thin, delicate peridium, then naked and ± pulverulent. – **Urediniospores** borne singly, short-pedicellate, broadly obovoid or ellipsoid (sometimes clavoid or pyriform), 20–35 × 10–22 µm; wall hyaline, thin (1–1.5 µm thick), finely verrucose-echinulate, with 4 indistinct, equatorial germ pores; contents orange-coloured. – **Amphispores** 20–38 × 15–28 µm, obovoid, broadly ellipsoid or nearly globoid, slightly angular; wall 1.3–5 µm thick, hyaline, with faint warts, and with 4–8 distinct, scattered germ pores; contents orange. – **Telia** mostly hypophyllous, on yellowish-brown to brown areas. – **Teliospores** formed within the abaxial epidermis cells, often filling the cells completely, 2- to many-celled by anticlinal septa; each cell about 14–18 µm in diam.; walls thin (1 µm or less), smooth, hyaline; 1 germ pore perceptible at the upper end of each cell; germination occurs without dormancy. – References: Gäumann (1959: 38–39), Wilson and Henderson (1966: 28–29).

Remarks. Urediniospores of both kinds (thin-walled urediniospores and amphispores) have been found in the same sori. Spores intermediate between thin-walled urediniospores and amphispores frequently occur. Amphispores usually appear later than thin-walled urediniospores, and predominate in some sori. Amphispores of *Hyalopsora aspidiotus* are much larger than those of *H. polypodii*. For transmission electron micrographs of the pointed warts of the urediniospores of *H. polypodii* see Berndt (1993), for the irregular shape of the teliospores see Berndt (1993, 1999a). – For records of *H. polypodii* in Austria see Poelt and Zwetko (1997: 68–69).

Melampsorella J. Schröt. emend. Berndt

Accumulating molecular genetic evidence might lead to a more stable concept of the genus *Pucciniastrum* and to inclusion of *Melampsorella*. Currently this genus is monotypic and characterised by the production of 'witches' brooms' on *Abies* and uredinia and telia on Caryophyllaceae. Formerly, it also contained *Melampsorella symphyti*, a species transferred to *Thekopsora* by Berndt (1993) and recently to *Pucciniastrum* by Padamsee and McKenzie (2014, see below).

Initially, *Melampsorella* was separated from *Thekopsora* and '*Pucciniastrum* s.l.' only on the basis of the number of teliospore cells and the pigmentation of the teliospore wall. Thus, it was based on rather variable characters. *Melampsorella* differed from *Thekopsora* by mostly 1-celled, thin-walled, almost hyaline teliospores lacking conspicuous germ pores. In *Thekopsora* teliospores are generally several-celled, with rather thick, pigmented walls, and an apical germ pore. *Melampsorella* and *Thekopsora* differed from our '*Pucciniastrum* s.str.' mainly by intraepidermal teliospores.

In addition to molecular genetic characters, the ultrastructure of haustoria and of the haustorial neck might still play an important role in the systematics of the Melampsorineae (Berndt 1993; Berndt and Oberwinkler 1995). Among the former 'Pucciniastraceae s.l.', for instance, only the genera *Milesina* and *Uredinopsis* (Milesinaceae) show the same type of haustoria as *Melampsorella elatina*.

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

1 *Melampsorella elatina* (Alb. & Schwein.) Arthur

Fig. 66

Syn. *Melampsorella caryophyllacearum* J. Schröt.; *M. caryophylleacearum* (DC.) J. Schröt. (orthogr. var.); *M. cerastii* (Pers.) J. Schröt.; *Melampsoridium caryophyllacearum* (J. Schröt.) Blanchette & Biggs

Hetereu-form:

0,I on: *Abies alba*, (*A. balsamea*, *A. cephalonica*, *A. concolor*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*, *A. veitchii*)

II,III on: *Cerastium arvense*, *C. fontanum*, *Dichodon cerastoides* [syn. *Cerastium c.*], *Rabelera holostea*

[syn. *Stellaria h.*], *Stellaria aquatica* [syn. *Myosoton aquaticum*], *S. graminea*, *S. nemorum*, (*Arenaria serpyllifolia*, *Cerastium alpinum*, *C. glomeratum*, *C. glutinosum*, *C. holosteoides*, *C. latifolium*, *C. pumilum*, *C. semidecandrum*, *Moehringia trinervia*, *Stellaria alsine*, *S. media*, *S. palustris*)

Spermatogonia on needles of current season, amphigenous, mostly epiphyllous, scattered, subcuticular, 90–320 µm in diam., 25–60 µm high, honey-coloured. Affected needles are shorter and paler (yellowish-green). – **Aecia** peridermioid, on needles of current season, hypophyllous, ± placed in two longitudinal rows, subepidermal in origin, erumpent, hemispherical or short-cylindrical, at first with a firm peridium, 0.4–1 mm high, 0.2–0.8 mm in diam., then rupturing irregularly at the apex; spore mass (yellowish-)orange; wall of peridial cells hyaline, thin; inner walls verruculose, outer walls smooth. – **Aeciospores** subgloboid, ellipsoid or polygonal, 16–30 × 14–17(–20) µm; wall hyaline, 1–2 µm thick, densely verrucose in face view and striate in optical section; without smooth areas; contents orange. – **Uredinia** hypophyllous, rarely epiphyllous or on petioles, small, 0.1–0.4 mm in diam., subepidermal, usually arising below a stoma, in groups or scattered, sometimes over the whole leaf surface, with ± hemispherical, delicate peridium, long covered by the epidermis, when mature opening by a pore, orange-yellow; wall of peridial cells (1.5–)2–3 µm thick, smooth, nearly hyaline. – **Urediniospores** borne singly on short pedicels, ellipsoid or ovoid, 16–30 × 12–21 µm; wall hyaline, 1–1.5 µm thick, sparsely echinulate; germ pores minute, 2–4, usually 2 towards each end; contents orange-yellow. – **Telia** hypophyllous, rarely epiphyllous, often covering the whole surface of the leaf on whitish or pale reddish areas. – **Teliospores** unstalked, formed within the epidermis cells, solitary or in groups, usually 1-celled, sometimes 2-celled, globoid, ellipsoid or sometimes angular, 12–25 µm across; wall thin (less than 1 µm), smooth, hyaline; contents almost hyaline or pale yellowish. – References: Gäumann (1959: 74–75), Wilson and Henderson (1966: 43–44).

Remarks. *Melampsorella elatina* induces the production of 'witches' brooms' on its aecial host. At first infected areas are recognisable as elongate swellings. Their surface becomes rough and cracked. In the following year, buds give rise to infected shoots, which form a broom. Brooms grow vertically upward, and usually continue to grow for a number of years and become very large in size. Usually, the infected needles fall already during the first year. Therefore, the witches' broom is bare in winter. If the stem becomes infected as well, a so-called 'Räder-tanne' can be seen. Then the rust induces a thickening of the trunk. After some years, the cortex dies.

On the uredinial and telial hosts the mycelium grows up with the young shoots and gradually extends into all the leaves, making them in some cases smaller and giving them a slightly yellowish appearance. In this rust the mycelium of both stages is perennial. Due to the therefore long-lasting infectivity mainly by urediniospores, the fungus can also survive and even propagate outside the distribution area of the aecial hosts. Hence, this rust is not bound to a specific plant association. In contrast to the rather conspicuous haplophase often observed with *Abies alba*, there are by far less reports of the dikaryophase in Austria. – For records of *M. elatina* in Austria see Poelt and Zwetko (1997: 85–86, as *M. caryophyllacearum*).

Melampsoridium Kleb.

The small genus alternates between *Larix* spp. (aecial hosts) and members of the Betulaceae (uredinial and telial hosts). In Austria aecia and spermatogonia have not been found. This might be explained by the inconspicuous appearance and short duration of the aecial stage (Wilson and Henderson 1966). – **Spermatogonia** subcuticular, ± flattened-conical (group I, type 3, according to Cummins and Hiratsuka 2003). – **Aecia** on the under surface of the needles, subepidermal in origin, erumpent, with blister-shaped peridium, which ruptures irregularly. – **Aeciospores** catenulate; wall thin, verrucose except for a smooth spot; contents reddish-yellow. – **Uredinia** hypophyllous, subepidermal in origin, with hemispherical peridium opening by an apical pore; ostiolar cells extending into an acute or acuminate, conical, spine-like apex; spore mass yellow-orange, soon bleaching out. – **Urediniospores** borne singly on pedicels; wall hyaline, echinulate, but in some species smooth at the apex. – **Telia** mostly hypophyllous, subepidermal, not erumpent, forming small crusts, which are one spore deep; crusts at first waxy-yellow or orange, then yellowish-brown or blackish. – **Teliospores** sessile, 1-celled, compacted laterally in a single layer; wall thin, smooth, nearly hyaline; germ pores often indistinct, probably 1 per cell; germination occurs in spring on fallen leaves.

Key to the *Melampsoridium* species in Europe

1a Urediniospores uniformly echinulate; germ pores 4–6, bizonate, 2–3 in subapical position and 2–3 close to the basal end of the spore; on *Alnus* sect. *Gymnothyrsus* (*Alnus* subgen. *Alnus*), in Austria on *A. incana* und *A. glutinosa* ..... *M. hiratsukanum*

1b Urediniospores with a smooth area at the apex 2

2a Urediniospores with 2–5, supraequatorial germ pores; on *Carpinus* ..... *M. carpini*

2b Urediniospores with 4–6, bizonate germ pores, 2–3 in subapical position and 2–3 close to the basal end of the spore; frequently on *Betula* and rarely on *Alnus* ..... *M. betulinum*

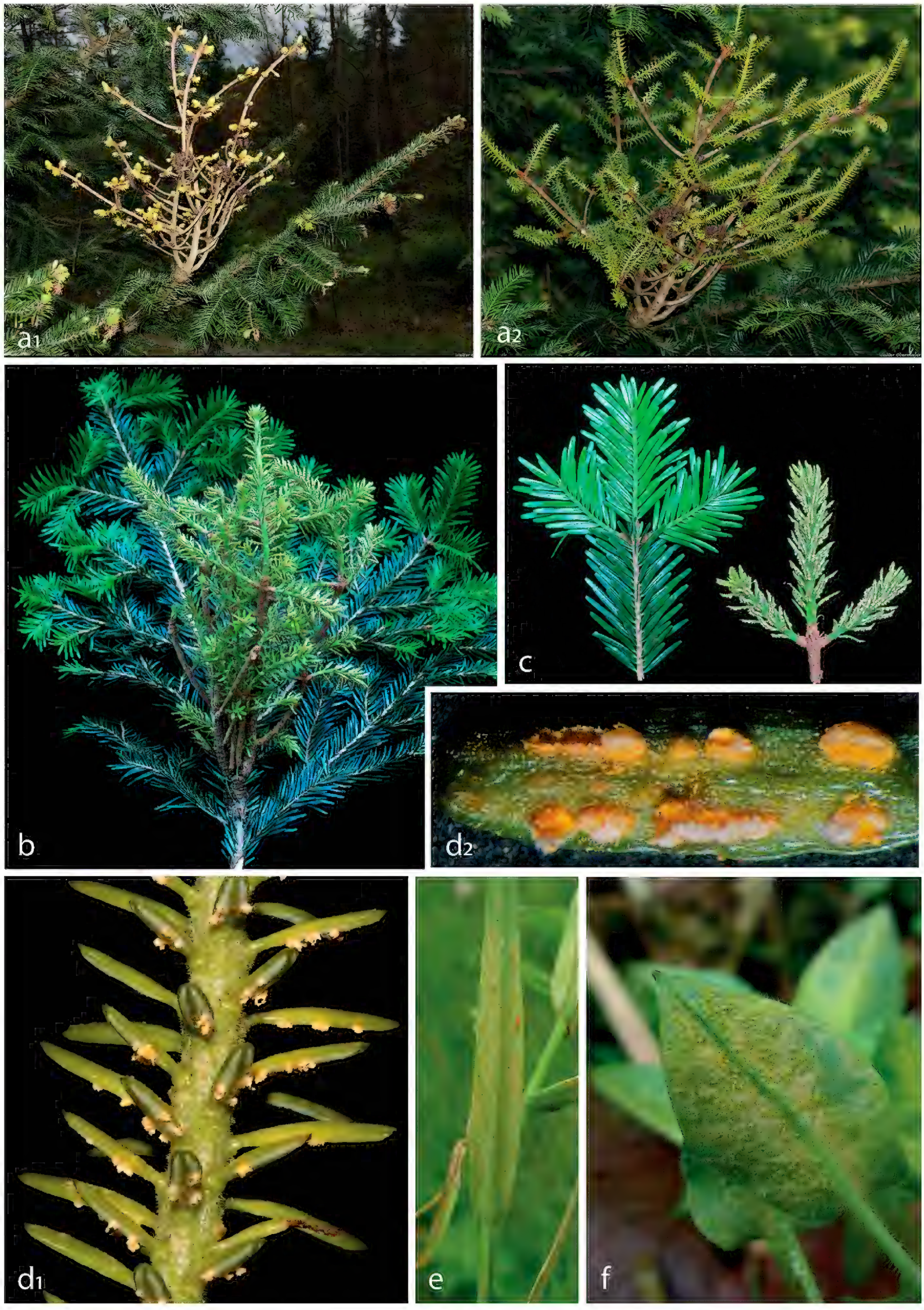


Figure 66. *Melampsorella elatina*. **a–d.** On *Abies alba*: **a1, a2.** Witches' broom with unfurling shoots in spring and with fully developed needles in early summer, originating from the upper side of a healthy branch; **b.** Smaller witches' broom; **c.** Comparison of a healthy twig (left) and an infected twig with aecia; **d1, d2.** Aecia hypophyllous, with orange spore mass; **e–f.** Uredinia on Caryophyllaceae: **e.** On *Rabelera holostea*; **f.** On *Stellaria nemorum*; (**a, d1** by Walter Obermayer; **e, f** by Julia Kruse).

1. *Melampsoridium betulinum* (Pers.) Kleb.

Fig. 67

Hetereu-form, in Austria probably often persisting as hemi-form:

(0,I on: *Larix decidua*, *L. kaempferi*)

II,III on: *Betula humilis*, *B. pendula*, *B. pubescens*, (*B. nana*, *B. papyrifera*)

In inoculation experiments, but rarely in nature:

(II,III on: *Alnus alnobetula*, *A. glutinosa*, *A. incana*) – For inoculation experiments in Norway see Roll-Hansen and Roll-Hansen (1981).

Spermatogonia on both sides of the needles, subcuticular, ± flattened-conical, 100–150 µm in diam., 50–65 µm high, pale yellow. – **Aecia** on the under surface of the needles, subepidermal, solitary or in longitudinal rows on one or both sides of the midrib; peridium blister-shaped, 0.5(–1.5) mm long, 0.25 mm wide and about 0.5 mm high (after Klebahn 1914, Gäumann 1959, and Majewski 1977), 0.3–1 mm long, 0.1–1.5 mm wide and 0.3–0.5 mm high (after Wilson and Henderson 1966), after rupturing with irregularly torn margin; peridial cells small, outer wall about 1 µm thick or thicker, nearly smooth, inner wall 3–4 µm thick, distinctly striate; spore mass (reddish-)orange fading to white. – **Aeciospores** globoid or ellipsoid, 14–24 × 11–18 µm, orange when fresh; wall hyaline, up to 2 µm thick, finely and closely verrucose except for a small smooth and slightly thinner area on one side. – **Uredinia** hypophyllous, scattered, sometimes covering the whole surface, yellow, small, 0.1–0.5 mm in diam., producing yellow spots on the upper side of the leaf; peridia hemispherical, firm, opening by an apical pore; peridial cells small, polygonal or rectangular, inner walls distinctly thickened (up to 8 µm); ostiolar cells ovate-conical, extending into an acute, spine-like apex, 23–30 µm long (after Szabó 2002a, b), 28–49 µm long (after Roll-Hansen and Roll-Hansen 1981). Roll-Hansen and Roll-Hansen (l.c.) emphasised that the maximum length of ostiolar cells varied from collection to collection. – **Urediniospores** oblong-ellipsoid or subclavate, 22–40 × 8–15 µm, mean 28.58 × 12.42 µm (after Szabó 2002a, b); mean 31.6 × 13.6 µm on *Betula pendula* and 33.6 × 15.0 µm on *B. pubescens* (after Kurkela et al. 1999); wall hyaline, 1.5–2 µm thick, echinulate, except for a smooth area at the apex; distance of spines about 3 µm; germ pores 4–6, bizonate (2–3 subapical, 2–3 close to the basal end of the spore). – **Telia** hypophyllous, subepidermal, scattered, sometimes covering the intercostal areas on the whole surface, small, about 0.5 mm in diam., at first orange, then brown. – **Teliospores** prismatic, 30–50 × 7–15 µm, rounded at both ends, arranged in a palisade-like layer; wall 1 µm thick at sides, up to 2 µm at the apex, nearly hyaline, smooth; germ pore indistinct. – References: Klebahn (1914: 817–818), Gäumann (1959: 68–69), Wilson and Henderson (1966: 49–50), Majewski (1977: 94–96), Roll-Hansen and Roll-Hansen (1981: 82), Kurkela et al. (1999: 989–990).

Figure 67. *Melampsoridium betulinum* on *Betula pendula*: **a.** Epiphyllous leaf spots; **b.** Hypophyllous uredinia; (**a, b** by Julia Kruse).

Remarks. Several authors (e.g., Wilson and Henderson 1966; Poelt 1985) hypothesised that *Melampsoridium betulinum* can persist without host alternation. Its uredinia or mycelia might outlast inside buds or young shoots of birches. In suitable places, it can develop in high quantities. Klebahn (1904) suggested that two specialised forms exist within this species: f.sp. *betulae-verrucosae* Kleb. infects *Betula pendula*, and f.sp. *betulae-pubescentis* Kleb. infects *B. pubescens* and *B. nana*. But these forms are not sharply differentiated. On *Alnus*, *M. betulinum* is reported only rarely from N and NW Europe (Roll-Hansen and Roll-Hansen 1981), Romania and Italy(?). *Melampsoridium hiratsukanum* also infects *Alnus* species but differs from *M. betulinum* by smaller and uniformly echinulate urediniospores which are broader and more circular. For nomenclatural comments on *M. betulinum* see Laundon and Holm (1976). – According to Poelt and Zwetko (1997: 86), *M. betulinum* is widespread in Austria and sometimes abundant in suitable localities.

2 *Melampsoridium carpini* (Nees) Dietel

Life cycle insufficiently known, probably persisting as hemi-form:

II,III on: *Carpinus betulus*

Spermatogonia and aecia unknown. – **Uredinia** hypophyllous, orange-yellow when fresh, small, 0.1–0.25 mm in diam., producing yellow spots on the upper side of the leaf; peridia hemispherical, opening by an apical pore; ostiolar cells extending into an acute, spine-like apex; peridial cells rather small, inner walls thickened (up to

3–4 µm). – **Urediniospores** oblong-ellipsoid, or subclavate, 18–28 × 8–15 µm; wall hyaline, up to 2 µm thick, ± loosely echinulate, except for a smooth area at the apex; distance of spines 2(–3) µm; germ pores 2–5, supraequatorial. – **Telia** hypophyllous, occasionally amphigenous, subepidermal, small, roundish or irregularly angular, at first yellow, then yellowish-brown. – **Teliospores** arranged in a palisade-like layer, prismatic, oblong or clavate, 18–25(–47) × 9–16 µm, yellowish-brownish, later blackish-brown; wall uniformly thick (about 1 µm). – References: Klebahn (1914: 820), Gäumann (1959: 72), Kaneko and Hiratsuka (1983: 2–3).

Remarks. Klebahn (1914) noticed that urediniospores occasionally remain viable during the winter. Hence, this rust can persist without host alternation, though the production of telia is rare. However, for a long time even the uredinial stage has been reported only rarely from Austria (Poelt and Zwetko 1997: 86–87). Only in recent years *Melampsoridium carpini* has become quite common, probably due to a change of climatic conditions, probably to the increased cultivation of susceptible horticultural varieties (*Carpinus betulus* cv. *columnaris*, cv. *fastigiata*), or both (e.g., Scheuer 2015).

From the Caucasian region of the former USSR also *Corylus avellana* is reported as host of *M. carpini* (Kuprevič and Uljaniščev 1975). From E Asia another species, *M. asiaticum* Kaneko & Y. Hirats., is known on *Ostrya* and *Carpinus*. To our knowledge no evidence is provided for the European *Ostrya carpinifolia* to serve as host for *Melampsoridium*. The corresponding information in Riegler-Hager et al. (2003) is erroneous.

3 *Melampsoridium hiratsukanum* S. Ito ex Hirats.f.

Fig. 68

Hetereu-form, in Austria mainly persisting as hemiform?

(0,I on: *Larix*)

II,III on: *Alnus glutinosa*, *A. glutinosa* × *incana*, *A. incana*

Spermatogonia inconspicuous, minute, without paraphyses. – **Aecia** subepidermal, cylindrical, 0.5–2 mm in diam., 1–2 mm high; peridial wall hyaline; peridial cells from quadrilateral to hexagonal, 22–35 × 13–20 µm in size. – **Aeciospores** intensely orange when fresh, roundish to elliptical, mean size 18.2–23.9 × 14.8–19.1 µm; wall hyaline, 1.8–2.0 µm thick, markedly verrucose. – **Uredinia** hypophyllous, scattered, sometimes covering the whole leaf surface, small, 0.1–0.3 mm in diam., producing yellow-reddish and later brownish-red spots on the upper side of the leaf; peridium hemispherical, firm, opening by an apical pore; ostiolar cells yellowish, ovate-conical, extending into an acute, spine-like apex 42–53 µm long (after Szabó 2002a, b); walls hyaline; spore mass bright orange when fresh, soon fading to white. – **Urediniospores** ellipsoid or subclavate, 20–34 × 8–15 µm, mean 26.24 × 11.46 µm (after Szabó 2002a, b), mean 25.0 × 14.0 µm on *Alnus incana* and 26.6 × 13.9 on *A. glutinosa* (after Kurkela et al. 1999); wall hyaline, up to 1 µm thick, uniformly echinulate; germ pores 4–6, bizonate (2–3 subapical, 2–3 close to the basal end of the spore). – **Telia** between, beside or under the uredinia, hardly larger than these, flat, orange. – **Teliospores** 1-celled or rarely 2-celled, 30–40 × 10–12 µm (after Riegler-Hager et al. 2003), 51–54 × 13–16 µm (after Müller 2003), arranged in a palisade-like layer, yellow; wall hyaline, about 1 µm thick at sides, up to 3 µm at the apex. – References: Kurkela et al. (1999: 989–990), Riegler-Hager et al. (2003: 136), Müller (2003: 282), Hantula et al. (2009), Moricca et al. (2021: 7–8).

Remarks. Collections of *Melampsoridium* on *Alnus glutinosa* and *A. incana* from Ireland, Scotland, Norway and Finland were identified as *M. betulinum* by Henderson and Bennell (1979) and Roll-Hansen and Roll-Hansen (1981). *Melampsoridium hiratsukanum* epidemics on alder occurred in Estonia for the first time in 1996 and in Finland in 1997 (Kurkela et al. (1999). In 1999 this rust was found on leaves of *Alnus incana* for the first time in Poland (Wołczańska 1999), in 2001 on *A. glutinosa* in Hungary (Szabó 2002a, b). A leaf rust epidemic on *A. glutinosa* and *A. incana*, caused by *M. hiratsukanum*, was observed in Austria for the first time in 1999. Hantula et al. (2009) confirmed that this new alder rust in Europe is conspecific to *M. hiratsukanum* in East Asia, also by ITS sequences. Moricca et al. (2021) recently described the aecia of *M. hiratsukanum* on *Larix* from northern Italy (Trento) and provided additional molecular genetic evidence for the identity of this invasive alder rust.

Usually, infected leaves of *Alnus incana* fall already during the summer, and heavily infested trees may be bare in September. In the Alps, this serious rust disease might cause environmental problems (like floods) because *Alnus incana* is one of the most important soil stabilisers along rivers and streams. – For detailed records of this invasive rust species in Austria see Riegler-Hager et al. (2003).

From Asia, *Melampsoridium alni* (Thüm.) Dietel is reported on *Alnus* sect. *Alnaster* (*Alnus* subgen. *Alnobetula*). The urediniospores of this species have two ± terminal germ pores, one at each spore end.

Pucciniastrum G.H. Otth

N.B.: In contrast to the original manuscript but according to recent molecular genetic evidence, we exclude the following genera from *Pucciniastrum*: *Thekopsora* Magnus (Coleosporiaceae), *Naohidemyces* S. Sato, Katsuya & Y. Hirats. (Milesinaceae), and *Calyptospora* J.G. Kühn. Accumulating evidence, however, might lead to inclusion of *Calyptospora* and *Melampsorella* in *Pucciniastrum*.

Some of the *Pucciniastrum* species included here produce aecia on *Abies* (Pinaceae), and uredinia and telia on *Circaea*, *Epilobium* (Onagraceae) and *Symphytum* (Boraginaceae). The aecial hosts and life cycles of the other species

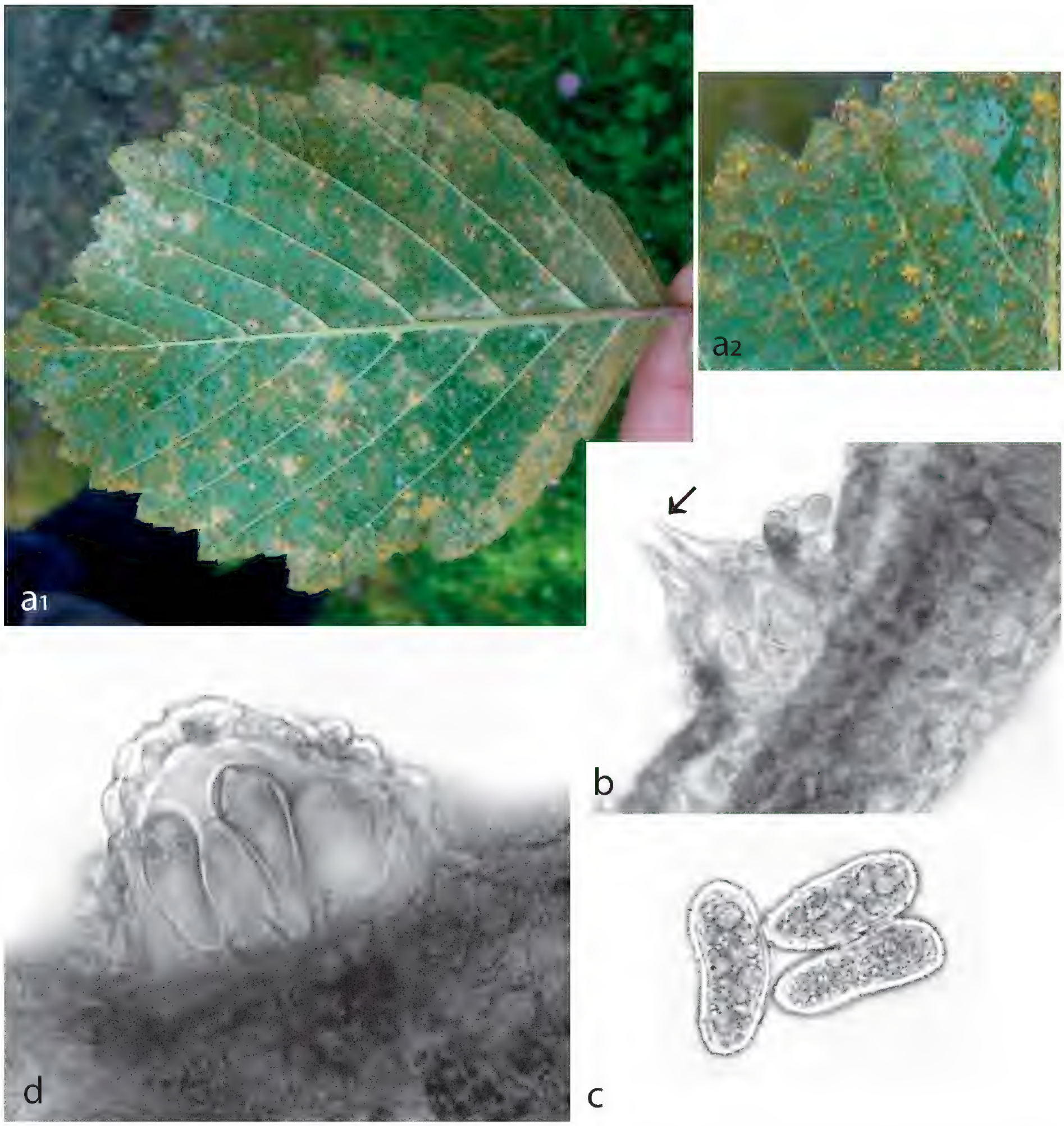


Figure 68. *Melampsoridium hiratsukanum* on *Alnus incana*: **a.** Uredinia hypophyllous, yellow-orange, but colour soon fading; **b.** Uredinium in vertical section; ostiolar cells forming a collar of long spines (arrow); **c.** Urediniospores; **d.** A small telium in vertical section; (**a** by Richard Tafner, with permission; **b–d** from Riegler-Hager et al. 2003: 137, with permission from the author, modified).

are apparently unknown. The following brief description is mainly based on Brandenburger (1985) and Cummins and Hiratsuka (2003). – **Spermatogonia** subcuticular, conical. – **Aecia** peridermioid, subepidermal in origin, erumpent; peridium well developed, cylindrical, rupturing longitudinally or irregularly at maturity. – **Aeciospores** catenulate; wall verrucose. – **Uredinia** subepidermal, pustular with hemispherical or conical peridium, opening by a pore, usually without distinct ostiolar cells. – **Urediniospores** borne singly on pedicels; wall hyaline, echinulate; germ pores scattered, obscure. – **Telia** 1 spore deep, consisting of sub- or intraepidermal crusts of laterally adherent teliospores, amphigenous. – **Teliospores** unstalked, 2- or usually more-celled by anticlinal septa, with 1 germ pore in the outer wall of each cell; wall pigmented.

Some remarkable morphological differences between our '*Pucciniastrum* s.str.' and other genera sometimes included in this genus (*Thekopsora*, *Naohidemyces*, *Calyptospora*, *Melampsorella*) are still found in the telia which are sub- or intraepidermal in *Pucciniastrum*, subepidermal in *Melampsoridium*, and intraepidermal in the other genera. The teliospores of some taxa also differ in the position of their germ pores (e.g., Cummins and Hiratsuka 2003). The known aecial hosts might be considered as

well: *Abies* in *Pucciniastrum*, *Calyptospora*, *Hyalopsora* and *Melampsorella*, *Larix* in *Melampsoridium*, *Picea* in *Thekopsora*, *Tsuga* in *Naohidemyces*.

However, the phylogenetic relationships within the former '*Pucciniastrum* s.l.' are more complicated than previous studies would suggest. For instance, Berndt and Oberwinkler (1995, 1997) examined the ultrastructure of haustoria (and the haustorial neck) as an important additional character for systematics and found that it splits both *Pucciniastrum* 's.str.' and *Thekopsora* into previously unknown subgroups. Molecular data soon confirmed that both are polyphyletic (Maier et al. 2003), but these results were not congruent with the ultrastructure data. For example, Berndt (1993) transferred '*Melampsorella*' *symphyti* (now *Pucciniastrum s.*) to *Thekopsora* because of the ultrastructure of its haustorial neck, but molecular data supported a close relationship with *Pucciniastrum guttatum* (Maier et al. 2003). *Pucciniastrum symphyti* and *P. guttatum* still form a weakly supported group together with *P. epilobii* and *P. circaeae* (Aime and McTaggart 2020). On the other hand, already Maier et al. (2003) found that there is no close affinity to a well-supported group currently placed in the genus *Thekopsora* (now a member of Coleosporiaceae, see Aime and McTaggart 2020): *Thekopsora areolata* (the type species of the genus), *Th. agrimoniae* and *Th. pyrolae*. To sum up, neither *Pucciniastrum* nor *Thekopsora* as treated by Cummins and Hiratsuka (2003) represented monophyletic groups, but satisfactory circumscriptions of the genera within Pucciniastraceae (especially *Pucciniastrum*) are still pending, also due to the uncertain justification of small genera like *Calyptospora* and *Melampsorella*, and to the weakly supported affiliation between the core group of *Pucciniastrum* on Onagraceae and the species on Boraginaceae (*P. brachybotrydis*, *P. symphyti*) and Rubiaceae (*P. guttatum*) (Aime and McTaggart 2020).

A key for all rust genera with aecia on needles of *Abies* is attached to *Milesina* (p. 250).

1 *Pucciniastrum brachybotrydis* (Tranzschel) Jørst.

Syn. *Thekopsora brachybotrydis* Tranzschel

Probably hemi-form:

II,III on: *Myosotis palustris* agg., (*Omphalodes*)

Spermatogonia and aecia unknown. – **Uredinia** mostly hypophyllous, in ± yellowish-brown leaf spots, pustular, with a hemispherical peridium, 0.2–0.38 mm in diam., brown. – **Urediniospores** 18–23 × 13.5–16 µm, ellipsoid to obovoid; wall hyaline, 1 µm thick, echinulate; contents golden yellow when fresh. – **Telia** mostly hypophyllous, in close vicinity to the uredinia, inconspicuous. – **Teliospores** formed within the epidermis cells, mainly 2(–5)-celled, 22–36 µm long and 14.5–29 µm wide when 2-celled, larger when more-celled, 18–25 µm high in vertical section; wall 1 µm thick, yellowish-brown, smooth. – Reference: Teppner et al. (1977: 281).

Remarks. For a long time, *Pucciniastrum brachybotrydis* has been known only from Asia. For the first report from Europe (Austria) see Teppner et al. (1977) and Poelt and Zwetko (1997: 252, as *Thekopsora b.*).

2 *Pucciniastrum circaeae* (Thüm.) Speg.

Fig. 69

Syn. *Uredo circaeae* Alb. & Schwein. [nom. illeg.]; *Melampsora circaeae* Thüm.; *Uredo circaeae* Schumach.

Hetereu-form:

(0,I on: *Abies alba*)

II,III on: *Circaea alpina*, *C. ×intermedia*, *C. lutetiana*

Spermatogonia amphigenous, subcuticular, sitting on the epidermis, 100–130 µm in diam., 25–35 µm high, yellow honey-coloured. – **Aecia** mostly hypophyllous, usually in two longitudinal rows, erumpent, cylindrical or clavoid, pale reddish, with a firm peridium, 0.25 mm in diam., up to 1 mm high, splitting irregularly at the apex; peridial cells white, with finely punctate walls. Spore mass pale yellow to bright orange. – Blumer (1963) has described the colour of the spore mass as pale yellow to pale orange and that of the single spore as hyaline to pale yellowish. – **Aeciospores** 14–32 × 11–21 µm; wall hyaline, about 2 µm thick and densely verruculose for the most part, often with a smooth strip where the wall is thinner. – **Uredinia** mostly hypophyllous, scattered or gregarious, in large pale leaf spots, often covering the whole surface, long covered by the epidermis, small, 0.1–0.2 mm in diam., pustular, with a hemispherical peridium, opening with a pore, pale yellow (to orange); ostiolar cells larger than other peridial cells, with smooth, slightly thickened walls (1.8–3 µm). – Scanning electron microscopy observation based on a large number of specimens from Japan showed that ostiolar cells are lacking (Liang et al. 2006: 141). – **Urediniospores** 18–24 × 12–14 µm; wall hyaline, 1–1.5 µm thick, minutely echinulate; contents orange-yellow when fresh. – **Telia** hypophyllous,

Figure 69. *Pucciniastrum circaeae* on *Circaea ×intermedia*: uredinia (photo by Julia Kruse).

subepidermal, very small, inconspicuous (scarcely visible to the naked eye). – **Teliospores** intercellular, single or in very small groups, formed underneath the epidermis or deeper in the host tissue, mostly divided into 4 cells by 2 anticlinal septa; in surface view 20–28 µm in diam. when 4-celled, 15–25 µm long and 12–20 µm wide when only 2-celled; in vertical section 16–21 µm high; wall evenly thick (about 2 µm), pale yellow, smooth. – References: Gäumann (1959: 46), Wilson and Henderson (1966: 34).

Remarks. The phylogenetic relationships of 14 morphologically similar species of *Pucciniastrum* distributed in Japan were analysed by Liang et al. (2006). Based on rDNA sequence data, *P. circaeae* and *P. epilobii* (s.l.? – see below) formed a highly coherent cluster, and were well separated from the other species investigated. These results agree with those of Maier et al. (2003). The urediniospores and teliospores of *P. circaeae* and *P. epilobii* are morphologically similar (Hiratsuka et al. 1992). Both species have very similar gymnopedunculate haustoria (Berndt and Oberwinkler 1995). Scanning electron microscopy observations showed that the uredinial peridia of both species lack ostiolar cells (Liang 2006). Based on these considerations, Liang et al. (2006) supposed that *P. circaeae* and *P. epilobii* may be conspecific.

However, European authors (e.g., Blumer 1963) reported that aeciospores of *P. circaeae* are larger than those of *P. epilobii*. According to Blumer (1963), aecia on *Abies alba* are rather common in Central Europe but have not been reported from Austria so far. – For records of *P. circaeae* in Austria see Poelt and Zwetko (1997: 249).

Pucciniastrum circaeae can be distinguished from *Puccinia* species on *Circaea* by its small, pustular, orange uredinia and its unstalked, intercellular teliospores. Aecia of *Puccinia circaeae-caricis* have cupulate white peridia when mature; telia of the microcyclic *Puccinia circaeae* are brown, cushion-like and confluent, with readily germinating teliospores (leptospores).

3 *Pucciniastrum epilobii* G.H. Otth s.str.

Syn. *Pucciniastrum abietis-chamaenerii* Kleb.; *P. epilobii* G.H. Otth f.sp. *abietis-chamaenerii* Kleb. [excl. *P. epilobii-dodonaei* Dietel & Eichhorn, *P. pustulatum* (Pers.) Dietel, and *P. fuchsiae* Hirats.f.]

Hetereu-form:

(0,I on: *Abies alba*, *A. balsamea*, *A. cephalonica*, *A. concolor*, *A. grandis*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*)

II,III on: *Epilobium angustifolium*, (*E. dodonaei* – inoculation experiments)

Spermatogonia hypophyllous, subcuticular, sitting on the epidermis, 45–210 µm in diam., 15–35 µm high. – **Aecia** on slightly paler needles of current season, hypophyllous, usually in two longitudinal rows, erumpent, cylindrical, with a firm peridium, about 0.25 mm in diam., up to 1 mm high and higher, splitting irregularly at the apex or rarely at the sides, whitish; peridial cells minutely verrucose on the inner walls; spore mass bright orange-yellow. – **Aeciospores** in chains with visible intercalary cells, 13–21 × 10–14 µm; wall hyaline, about 1.5 µm thick and minutely verrucose for the most part, often with an almost smooth spot where the wall is thinner (1 µm). – **Uredinia** mostly hypophyllous, later also epiphyllous, often on stems, scattered or in groups, in yellow or reddish leaf spots, long covered by the epidermis; small, about 0.25 mm in diam, pustular, with a hemispherical thin walled peridium, opening with a pore, yellow; ostiolar cells not distinctly differentiated from other peridial cells. – Scanning electron microscopy observation based on a large number of specimens from Japan showed that ostiolar cells are lacking (Liang et al. 2006: 141). – **Urediniospores** 14–24 × 11–17 µm; wall hyaline, 1(–1.5) µm thick, remotely short-echinulate. – **Telia** hypophyllous, rarely epiphyllous or on stems, subepidermal, small, 0.1–0.2 mm in diam., often in groups, which form pale reddish-brown (later blackish-brown) crusts. – **Teliospores** intercellular, formed underneath the epidermis, cylindrical to globoid, ± prismatic by the pressure of the compact mass of spores in the centre of the sori, (1–)2(–4)-celled; in vertical section 7–14 µm wide and 17–28 µm high (after Gäumann 1959); 18–28 × 7–15 µm when 2-celled, 20–30 µm in diam. when 4-celled (after Wilson and Henderson 1966); wall 1–1.5 thick at sides, up to 3 µm thick at the apex, brown, smooth, with 1 germ pore in the upper part. – References: Gäumann (1959: 41–42), Wilson and Henderson (1966: 31, 32).

Remarks. Gäumann (1959) discussed *Pucciniastrum epilobii* (s.l.) in detail and divided it into two 'specialised forms' (formae speciales), f.sp. *abietis-chamaenerii* Kleb. and f.sp. *palustris* Gäum. The present *P. epilobii* s.str. is identical with Gäumann's f.sp. *abietis-chamaenerii* and apparently confined to *Epilobium angustifolium* (our most common representative of subgen. *Chamaenerion*). Telia of *P. epilobii* s.str. are abundant and form conspicuous crusts, and the apical wall of the teliospores is regularly thickened, whereas telia of *P. pustulatum* are rare, small and inconspicuous, and the apical wall of the teliospores is not regularly thickened. Gäumann (1959) also discussed differences in teliospore ontogeny between the two forms. Moreover, Gäumann (1959) noted that host alternation with *Abies* is only proven for f.sp. *abietis-chamaenerii* (i.e., *P. epilobii* s.str.). – For records of *P. epilobii* s.str. in Austria see Poelt and Zwetko (1997: 249, as *P. epilobii* f.sp. *abietis-chamaenerii*).

4 *Pucciniastrum epilobii-dodonaei* Dietel & Eichhorn

Life cycle insufficiently known:

II,III on: *Epilobium dodonaei*

Spermatogonia and aecia unknown. – **Uredinia** ± covering the whole surface of the leaf. – **Urediniospores** 18–30 × 14–22 µm. – **Teliospores** 25–50 µm high and 8–17 µm wide. – Reference: Dietel and Eichhorn (in Sydow 1942: 196–197).

Remarks. The status of this taxon is uncertain. It differs from *Pucciniastrum epilobii* s.str. in the size of its spores and the habit of the affected plant. Because both

sides of the leaves are covered by numerous uredinia, infected plants are yellow in appearance. This might be due to host anatomy. – For a record of *P. epilobii-dodonaei* in Austria see Poelt and Zwetko (1997: 249).

5 *Pucciniastrum fuchsiae* Hirats.f.

Syn. *Uredo fuchsiae* Arthur & Holw. [non (Cooke) Henn.]

Life cycle insufficiently known:

II on: *Fuchsia* sp. cult.

Spermatogonia, aecia and telia unknown. – **Uredinia** hypophyllous, subepidermal, yellowish orange, orbicular, 0.1–0.2 mm in diam., thickly scattered in irregular groups on slightly swollen leaf areas; peridium hemispherical, at first opening by a small apical pore through which the uredospores are extruded, later rupturing to expose the pallid orange spore mass and remaining as a tattered fringe; ostiolar cells at the apex of peridia, rounded and smooth. – **Urediniospores** pedicellate, subglobose or ellipsoid or obovate, sometimes irregular, 15–23(–26) × (11–)13–17(–20) µm; wall hyaline, echinulate, uniformly thin (c. 1 µm); germ pores obscure. – References: McNabb and Laurenson (1965: 337–338), Poelt and Zwetko (1991: 71), Wahyuno et al. (2012: 144–145) as *P. epilobii*; Garibaldi et al. (2012), Ferrada et al. (2020) as *P. circaeae*.

Remarks. Infected leaves soon turn yellow and wilt, probably the reason why no telia are found on *Fuchsia*. Gäumann (1959) included this taxon in *Pucciniastrum epilobii* f.sp. *palustris*, but molecular genetic evidence has shown that it is phylogenetically close to *P. circaeae* and currently often synonymised with that species (e.g., Garibaldi et al. 2012; Scholler et al. 2022). Following Thiel et al. (2023) we prefer to treat *P. fuchsiae* as a separate species. – For a record in Austria see Poelt and Zwetko (1991; 1997: 249, under *P. epilobii* f.sp. *palustris*).

(6) *Pucciniastrum goodyerae* (Tranzschel) Arthur

Syn. *Uredo goodyerae* Tranzschel

Life cycle insufficiently known:

(II on: *Goodyera repens*)

Spermatogonia, aecia and telia unknown. – **Uredinia** amphigenous, scattered or crowded in small groups, long covered by the epidermis, 0.1–0.4 mm in diam., pustular, yellow-orange; peridium delicate, firm, hemispherical, opening with an apical pore; wall of peridial cells thin, smooth, almost hyaline or very pale yellowish; ostiolar cells rather large, 32–42 µm high, finely echinulate above. – **Urediniospores** 23–34 × 16–21 µm, ovoid, elongate or elongate-clavoid; wall uniformly thick (1.5–2 µm), finely echinulate, hyaline; contents yellow-orange when fresh. – References: Gäumann (1959: 52), Wilson and Henderson (1966: 42).

Remarks. The uredinia of this rust have sporadically been found on *Goodyera repens* in several locations of the N hemisphere but not in Austria so far.

7 *Pucciniastrum guttatum* (J. Schröt.) Hyl., Jørst. & Nannf.

Fig. 70

Syn. *Thekopsora guttata* (J. Schröt.) P. Syd. & Syd.; *Th. galii* (G. Winter) De Toni; *Pucciniastrum galii* (Link) E. Fisch.

Probably hemi-form (or hetereu-form?):

II,III on: *Galium mollugo* agg., *G. odoratum*, *G. pumilum*, *G. saxatile*, *G. sylvaticum*, *G. verum*, (*Asperula purpurea*, *Cruciata verna* [syn. *C. glabra*], *C. laevipes*, *Galium album*, *G. anisophyllon*, *G. aparine*, *G. aristatum*, *G. glaucum*, *G. palustre*, *G. pariense*, *G. ×pomeranicum*, *G. rivale*, *G. rotundifolium*, *G. intermedium* [syn. *G. schultesii*], *G. spurium*, *G. uliginosum*, *Sherardia arvensis*)

Spermatogonia and aecia unknown? – **Uredinia** hypophyllous, scattered or crowded, sometimes ± covering the whole leaf surface, pustular, with a hemispherical peridium, 0.1–0.25 mm in diam., opening with a pore, (yellow-)orange; ostiolar cells rounded, wall 1.5–2.5 µm thick, smooth, almost hyaline. – **Urediniospores** 13–24 × 10–18 µm; wall hyaline, 1–1.5 µm thick, echinulate; contents orange when fresh. – **Telia** amphigenous, forming small dark brown crusts, sometimes covering the whole leaf surface. – **Teliospores** formed within the epidermis cells, mainly divided into (2–)4 cells by anticlinal septa, 22–30 µm in diam., 21–24 µm high (in vertical section); wall 1–2 µm thick, thickened mainly at the apex, yellowish-brown, smooth, with 1 germ pore in each cell in the corner where the anticlinal walls meet. – Reference: Gäumann (1959: 64).

Remarks. *Pucciniastrum guttatum* can be distinguished from *Puccinia* species on *Galium* by its pustular uredinia and its unstalked, intraepidermal teliospores. Wilson and Henderson (1966) have confirmed the supposition of

Figure 70. *Pucciniastrum guttatum* on *Galium rotundifolium*: uredinia (photo by Julia Kruse).

Gäumann (1959) that *Pucciniastrum guttatum* perennates in the uredinial stage (probably by infected basal rosettes of the hosts). Uredinia on overwintered leaves of *Galium odoratum* have been found in Scotland in March. Hence the rust does not need alternation. Henderson (2004) reported that it alternates with *Abies*, but we do not know his sources. – For records of *Pucciniastrum guttatum* in Austria see Poelt and Zwetko (1997: 253, as *Thekopsora guttata*).

8 *Pucciniastrum pustulatum* (Pers.) Dietel

Syn. *Pucciniastrum epilobii* s.l.; *P. epilobii* G.H. Otth f.sp. *palustris* Gäum.

Life cycle insufficiently known:
(0,I on: *Abies alba*?, *Abies* spp.?)
II,[III] on: *Epilobium alsinifolium*, *E. collinum*, *E. montanum*, *E. palustre*, *E. parviflorum*, *E. roseum*, *E. tetragonum*, (*E. alpestre*, *E. anagallidifolium*, *E. ciliatum*, *E. dodonaei*?, *E. fleischeri*?, *E. hirsutum*, *E. obscurum*, *E. tetragonum* subsp. *lamyi*, *Godetia* sp. cult.)

Spermatogonia and Aecia unknown? – **Uredinia** and **urediniospores** as in *P. epilobii* s.str., but urediniospore wall slightly thinner (up to 1 µm). – **Telia** (if present) hypophyllous, rarely epiphyllous or on stems, subepidermal, small, 0.1–0.2 mm in diam., rare and inconspicuous (not confluent and crust-like as in *P. epilobii* s.str.). – **Teliospores** as in *P. epilobii* s.str., but their walls not regularly thickened at the apex. – References: Gäumann (1959: 41–46).

Remarks. *Pucciniastrum pustulatum* appears to be almost congruent with Gäumann's *P. epilobii* f.sp. *palustris* and has a much wider host range than f.sp. *abietis-chamaenerii* (*P. epilobii* s.str.). However, *P. fuchsiae* on *Fuchsia* spp. cult. is currently either kept as a separate species (see above) or united with *P. circaeae*. – For records of *P. pustulatum* in Austria see Poelt and Zwetko (1997: 249, as *P. epilobii* f.sp. *palustris*).

9 *Pucciniastrum symphyti* (DC.) McKenzie & Padamsee

Fig. 71

Syn. *Melampsorella symphyti* (DC.) Bubák; *Thekopsora symphyti* (Bubák) Berndt [nom. inval.]; *Th. symphyti* (Bubák) J. Müll.

Hetereu-form:
(0,I on: *Abies alba*)
II,III on: *Symphytum officinale*, *S. tuberosum*, (*S.* ×*uplandicum*)

Spermatogonia on needles of current season, mostly hypophyllous, crowded, often spread over the whole leaf

Figure 71. *Pucciniastrum symphyti* on *Symphytum tuberosum*: **a.** Uredinia hypophyllous, often covering the whole leaf surface; **b.** Close-up of uredinia.

surface, minute, yellowish-orange. – **Aecia** on needles of current season, hypophyllous, placed in two longitudinal rows, not crowded, cylindrical, 0.5–0.8 mm high; peridium firm, hyaline, rupturing longitudinally or irregularly at the apex, at length torn to the base into 3–5 segments; wall of peridial cells 2–2.5 µm thick, hyaline; spore mass yellowish-orange. – **Aeciospores** in chains with intercalary cells, 20–40 × 18–29 µm; wall hyaline, 1.5–2 µm thick, densely verrucose in face view and striate in optical section, sometimes with smooth areas; contents orange. – **Uredinia** hypophyllous, 0.1–0.3 mm in diam., evenly and densely covering the leaf surface, causing small, yellowish leaf spots on the upper surface, pustular, with a hemispherical peridium, long covered by the epidermis, which finally ruptures at a centrally placed pore; wall of peridial cells thin, smooth, hyaline or subhyaline. – **Urediniospores** golden yellowish-orange in mass, 22–35 × 16–28 µm; wall hyaline, 1–1.5 µm thick, sparsely and coarsely echinulate; germ pores inconspicuous. – **Telia** hypophyllous, intercellular, forming large whitish or pinkish patches. – **Teliospores** formed within the epidermis cells, usually interpreted as 1-celled (but many spores in each epidermis cell), 11–18 × 9–15 µm (8–20 µm in diam.); wall evenly thin (less than 1 µm thick), smooth, subhyaline or yellowish, probably with 1 inconspicuous germ pore. – Reference: Gäumann (1959: 78–79).

Remarks. Because of its haustorial ultrastructure *Pucciniastrum symphyti* has been transferred to *Thekopsora* by Berndt (1993). Molecular genetic data, however, support a close relationship between *P. symphyti* and *P. guttatum* (syn. *Thekopsora guttata*). But there is no close affinity of these two species to *Melampsorella elatina* (syn. *M. caryophyllacearum*), the type species of *Melampsorella* (Maier et al. 2003; Aime and McTaggart 2020). – For records of *P. symphyti* in Austria see Poelt and Zwetko (1997: 253–254, as *Thekopsora s.*).

Species incertae sedis

***Uredo* auct.**

Due to the morphology of the uredinia, the following taxon belongs to the Melampsorineae, most probably to the genus *Pucciniastrum*.

(1) *Uredo kriegeriana* Syd. & P. Syd.

Life cycle insufficiently known:

(II on: *Cannabis sativa*)

Spermatogonia, aecia and telia unknown. – **Uredinia** usually hypophyllous, scattered or in loose groups, long covered, yellowish, minute, on pale irregular leaf spots; peridium delicate; peridial cells 12–17 × 10–13 µm, roundish-angular or ellipsoid to ovoid-angular; wall of peridial cells uniformly thick, about 1 µm, smooth, hyaline. – **Urediniospores** 21–27 × 15–22 µm, subglobboid, ovoid or ellipsoid; walls 1.5 µm thick, hyaline, densely and finely echinulate; spines minute and short; germ pores obscure; contents orange. – References: Sydow and Sydow (1924: 500–501), Gäumann (1959: 20).

Remarks. This inconspicuous species is described from 'Sächsische Schweiz', Saxony (see Gäumann 1959). It is known from the type locality and has been reported two times and only on a few leaves. Poelt and Zwetko (1997) do not mention it.

Other families and Genera incertae sedis

In Cummins and Hiratsuka (2003), the genera of this chapter were placed in the families Chaconiaceae (*Ochropsora*), Uropyxidaceae (*Leucotelium*, *Tranzschelia*), Raveneliaceae (*Nyssopsora*, *Triphragmiopsis*), and Pucciniaceae (*Gymnosporangium*). But this system does not correspond with classifications based on molecular genetic data (e.g., Maier et al. 2003; Aime 2006; Aime et al. 2018a; Aime and McTaggart 2020). Therefore, we also accept some narrowly delimited families; the brief descriptions of Gymnosporangiaceae, Ochropsoraceae and Tranzscheliaceae are cited here from Aime and McTaggart (2020). *Nyssopsora* and *Triphragmiopsis* are treated as Genera incertae sedis, for the time being.

Gymnosporangiaceae Chevall. (Isonym: Gymnosporangiaceae P. Zhao & L. Cai emend. Aime & McTaggart)

The following brief description is cited from Aime and McTaggart (2020: 41): "Spermogonia Group V (type 4). Aecia roestelia-type (*Gymnosporangium*) or less frequently aecidium-type (*Gymnotelium*). Teliospores mostly 2-celled, germinating without dormancy via external basidia. Life cycles mostly demicyclic [opsis-form] and heteroecious (*Gymnosporangium*)."

***Gymnosporangium* R. Hedw. ex DC.**

Syn. *Roestelia* Rebent.

This genus represents heteroecious rusts with Rosaceae ('Maloideae') as alternate hosts and species of *Juniperus* (in Europe) as telial hosts. Ten species are recorded from Europe; two further species (*G. asiaticum* and *G. juniperi-virginianae*) have been introduced some decades ago, but did not persist. The genus is well characterised by its host specificity and unique morphological characters like roestelioid aecia and gelatinous telia. It is the only rust genus which forms telia on gymnosperms regularly (Leppik 1973). – **Spermatogonia** subepidermal (Group V, type 4, according to Cummins and Hiratsuka 2003), globose or subglobose, yellow-orange, becoming

blackish-brown. – **Aecia** roestelioid, subepidermal in origin, erumpent; peridia conspicuous, at first cylindrical and closed at the apex, generally tending to rip longitudinally at maturity; peridium cells with characteristic ornamentation (Fig. 73). – **Aeciospores** catenulate; walls verrucose, usually pigmented, with distinct scattered germ pores. – **Uredinia** (if present) subepidermal in origin, erumpent, ± pulverulent; lacking in most species. – **Urediniospores** borne singly on pedicels; walls verrucose; germ pores scattered. – **Telia** subepidermal in origin, erumpent, at first brown, cushion-, crest- or horn-shaped, when moistened, swelling strongly and becoming orange(-brown), gelatinous, tongue-shaped or conical. – **Teliospores** (Fig. 72) borne singly on pedicels, 1- to several-celled but mostly 2-celled, biconical, ellipsoid, lanceolate or fusiform, not or slightly constricted at septa; germ pores 1 to several but usually 2 per cell; wall smooth, often pigmented; pedicels often rather long, in most species gelatinising when moist. – Usually, the mycelium in juniper stems, branches and evergreen leaves is perennial and causes swelling or fasciation. Germination of teliospores occurs without dormancy. Under moist conditions, gelatinisation of their long pedicels and production of basidia and basidiospores take place concurrently and very rapidly. Shape and size of teliospores vary considerably according to their position in the sorus.

Based on the spermatogonia morphology, the genus *Gymnosporangium* has been placed in the family Pucciniaceae (Cummins and Hiratsuka 2003). Molecular data do not confirm this placement. Maier et al. (2003) and Aime (2006) show that the genus represents a monophyletic group separate from Pucciniaceae s.str.

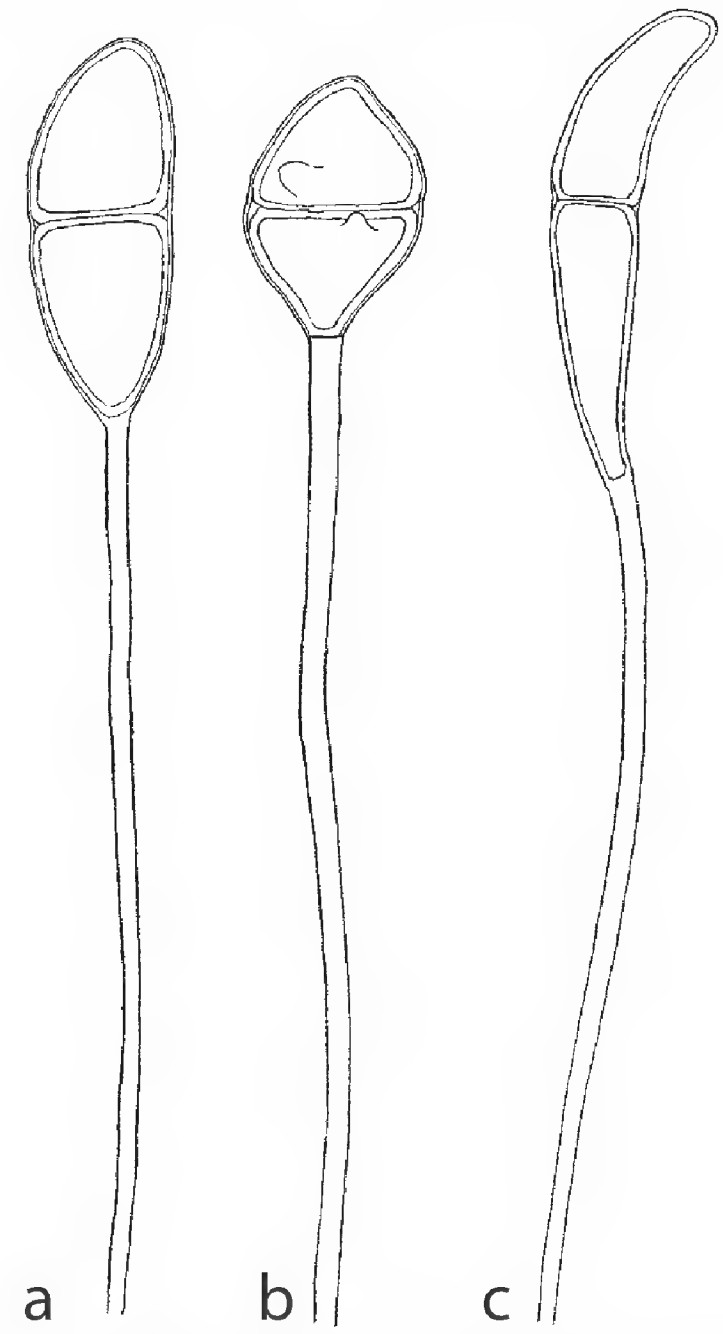


Figure 72. *Gymnosporangium* spp., types of teliospores. **a.** *G. tremelloides*, spores ellipsoid, spore ends roundish; **b.** *G. cornutum*, spores smaller and often biconical; **c.** *G. clavariiforme*, spores fusiform; (**a–c** from Dietel 1928: 75, with permission from Duncker & Humblot GmbH).

Key to the *Gymnosporangium* species on *Juniperus* in Central Europe

(Fig. 72)

1a Uredinia on needles, ± pulverulent; teliospores in the uredinia ..... *G. gaeumannii*
1b Uredinia lacking, telia gelatinous when moist (see **Note 1** below) 2
2a Telia on *Juniperus communis* (incl. subsp. *nana*) 3
2b Telia on *J. sabina*, *J. chinensis* and related species (*J.* sect. *Sabina*) 6
3a Teliospores lanceolate or fusiform, 50–110(–120) × (10–)15–21 µm ..... *G. clavariiforme*
3b Teliospores short-fusiform, oval or biconical, 30–70 × 15–32 µm 4
4a Telia on branches, rather large, up to 20 mm long (before swelling and becoming gelatinous), teliospores 35–70 × 20–30 µm ..... *G. tremelloides*
4b Telia on branches and leaves, smaller, up to 5 mm long (before swelling and becoming gelatinous) ..... (*G. cornutum* s.l.) 5
5a Telia on leaves, teliospores 35–49 × 21–30 µm ..... *G. torminali-juniperini*
5b Telia on branches, occasionally on leaves, teliospores 30–55 × 15–32 µm .... *G. cornutum* s.str., *G. amelanchieris*
6a Teliospores fusiform, 46–90 × 16–24 µm, with 1 germ pore per cell ..... *G. fusisporum*
6b Teliospores oval or biconical, 35–50 × 18–30 µm, with 2 germ pores per cell 7
7a Teliospores bluntly conical at apex ..... *G. sabinae*
7b Teliospores rounded at apex ..... *G. confusum*

Note 1: Under dry conditions, telia of *Gymnosporangium confusum* and *G. sabinae* are cushion- or horn-shaped, usually higher than wide; in contrast, telia of *G. amelanchieris*, *G. cornutum*, *G. torminali-juniperini* and *G. tremelloides* are much wider than high.

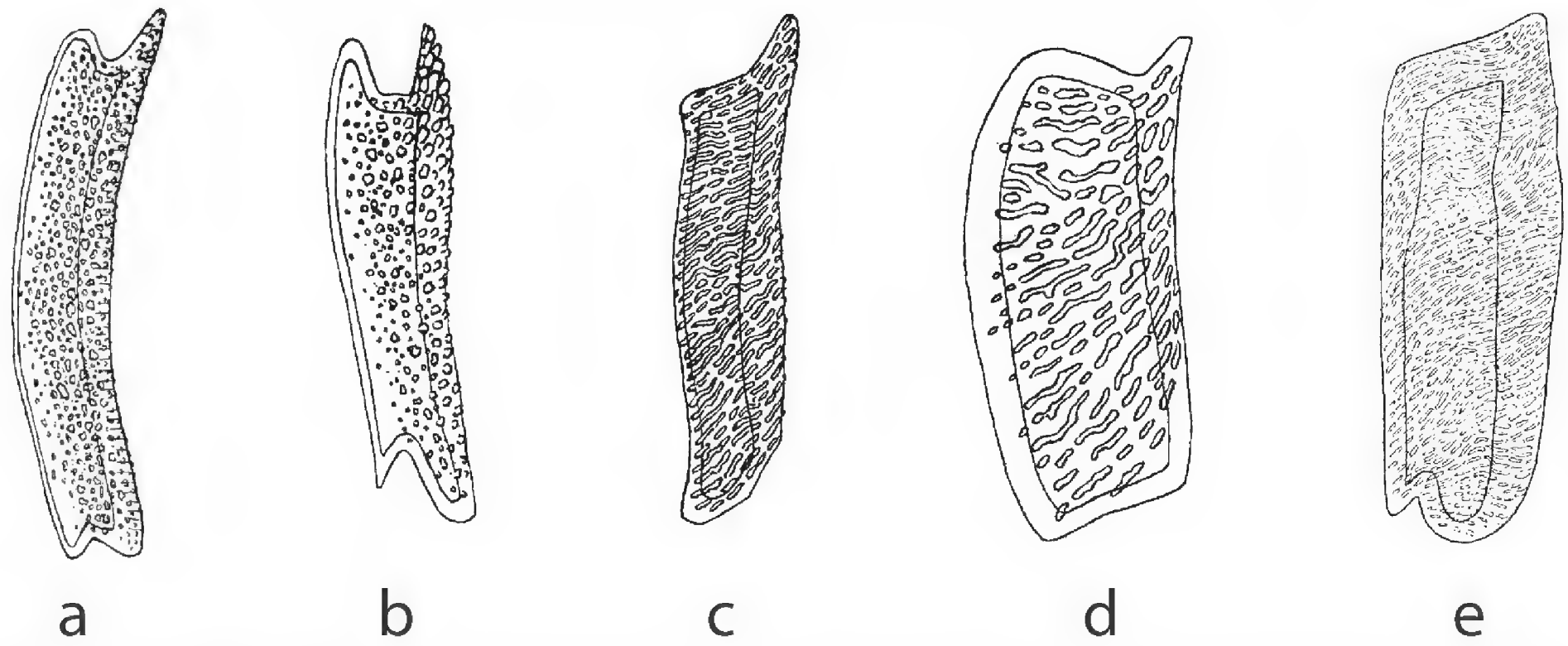


Figure 73. *Gymnosporangium* spp., ornamentation of lateral walls of peridial cells of aecia. **a.** *G. clavariiforme*; **b.** *G. sabinae*; **c.** *G. confusum*; **d.** *G. tremelloides*; **e.** *G. cornutum*. In **a** and **b** with roundish papilla-like warts of different size; in **c, d** and **e** with elongate ridges of different size and density, but rather coarse in **d**; (**a–e** from Klebahn 1914: 646, 666, **d** as *G. ariae-tremelloides*, **e** as *G.* (*aucupariae-*)*juniperinum*).

Key to *Gymnosporangium* species in the aecial stage

(Fig. 73)

1a Peridia not opening at the apex, laterally bulging and splitting into fibers which remain united at the apex ..... *G. sabinae*
1b Peridia soon opening at the apex 2
2a Peridia rather long, up to 5 mm, cornute, hardly fringed at the summit ..... (*G. cornutum* s.l.) 3
2b Peridia soon lacerate nearly to base or fimbriate in upper half, fringed in appearance 4
3a Mainly on *Amelanchier ovalis* ..... *G. amelanchieris*
3b Mainly on *Sorbus aucuparia* and *S. hybrida* ..... *G. cornutum*
3c Mainly on *Sorbus torminalis* ..... *G. torminali-juniperini*
4a Peridia rather long, up to 5 mm; side walls of peridial cells with elongate warts and ridges; aeciospores 19–35 × 18–24 µm ..... *G. fusisporum*
4b Peridia shorter, 0.5–3 mm long 5
5a Side walls of peridial cells with elongate warts and ridges; aeciospores 19–27 × 19–22 µm ..... *G. confusum*
5b Side walls of peridial cells with elongate and rather broad warts and ridges which do not extend to the outer margin; aeciospores rather large, 30–50 × 25–35 µm ..... *G. tremelloides*
5c Side walls of peridial cells with roundish, papilla-like warts of varying size; aeciospores 25–29 × 18–23 µm ..... *G. clavariiforme*

1 *Gymnosporangium amelanchieris* E. Fisch. ex F. Kern

Syn. *Gymnosporangium cornutum* Arthur ex F. Kern f.sp. *amelanchieris* E. Fisch.; *G. juniperinum* (L.) Fr. f.sp. *amelanchieris* E. Fisch.

Heteropsis-form:

0,I on: *Amelanchier ovalis*, (*A. asiatica*, *Pyracantha coccinea*)

III on: *Juniperus communis*, (*J. communis* subsp. *nana*)

Spermatogonia epiphyllous, subepidermal, only the upper part protruding as a distinct cone, first yellowish, becoming black; in the centre of large leaf discolourations. – **Aecia** hypophyllous on conspicuously swollen leaf tissue; peridia cornute, long (3–5 mm), opening at apex, becoming split along the sides; peridial cells rhomboid in lateral view, 29–39 µm thick, 80–100 µm long; outer wall 2–3 µm, inner and side walls 7–9 µm thick; rather loosely rugose with elongate papillae and ridges of varying length. – **Aeciospores** globoid, 25–29 × 18–23 µm; wall 1.5–2.5 µm thick, light brown, 'verrucose' (approx. 1.1 warts/µm²); germ pores 6–10; contents hyaline. – **Telia** caulicolous, on swellings, less often on needles, small on the latter (1–2 mm in diam.), somewhat bigger on branches (3–5 mm in diam.); spore mass at first applanate and brown, then, when moist, swelling and becoming gelatinous. – **Teliospores** 2-celled, 35–55 × 19–32 µm, light brown; germ pores 1–2 per cell, apical or near septum. – Reference: Helfer (2005: 335).

Remarks. Gäumann (1959) considers this rust as a forma specialis of *Gymnosporangium juniperinum*, and

Kern (1973a) treats it as f.sp. of *G. torminali-juniperini*. *Gymnosporangium amelanchieris* differs from *G. torminali-juniperini* in less thickened side walls and less densely rugose ornamentation of peridial cells (Helfer 2005). Its teliospores are slightly larger than those of *G. cornutum* s.str. and have less distinct papillae over the germ pores.

Lee and Kakishima (1999) characterise the aeciospore surface ornamentation of *G. amelanchieris* as minutely coronate. The basal parts of the processes ('warts') are columnar, and upper parts are divided into small protuberances (for scanning electron micrographs of aeciospores see Lee and Kakishima 1999: 116, fig. 3A, B).

For records of *G. amelanchieris* in Austria see Poelt and Zwetko (1997: 64–65). *Amelanchier ovalis* is also attacked by *G. clavariiforme* and, in S Europe, by *G. gracile* Pat., but the telial host of the latter does not occur in Austria.

2 *Gymnosporangium clavariiforme* (Wulfen) DC.

Figs 72c, 73a

Syn. *Gymnosporangium clavariaeforme* (Jacq.) DC. (orthogr. var.)

Heteropsis-form:

0,I on: *Amelanchier ovalis*, *Cotoneaster integerrimus*?, *Crataegus laevigata*, *C. monogyna*, (*C. lindmanii* [syn. *C. rhipidophylla* subsp. *l.*], *Pyracantha coccinea*, *Pyrus communis*)

0,[I] on: *Sorbus aucuparia*?, (*Cydonia oblonga*, *Malus domestica*, *Sorbus aria*?, *S. latifolia*, *S. torminalis*) – less susceptible hosts

III on: *Juniperus communis*, (*J. communis* subsp. *nana*)

Spermatogonia in the centre of red leaf spots, chiefly epiphyllous, but also on fruits, subepidermal, only upper part protruding as distinct cone (110 µm wide, 130–140 µm high), first yellowish, then becoming dark brown. – **Aecia** hypophyllous, but also on stems and fruits, in the centre of yellow, then red or brown and ± swollen spots; peridia 0.5 mm wide, 2–3 mm long, tubular, soon becoming lacerate almost to the base, fimbriate above, whitish-yellow; peridial cells long (80–130 µm) and narrow; outer wall smooth, 1–2 µm thick; inner and side walls thickened (5–7 µm), rather densely covered with rounded papillae of varying size. – **Aeciospores** 25–29 × 18–23 µm, globoid; walls 1.5–3 µm thick, light brown, densely verrucose (1.1 warts/µm^2); germ pores 6–10. – **Telia** on elongate, fusiform swellings of the branches (on *J. communis* subsp. *nana* also on needles); under dry conditions small, yellowish-brown, rather hard and brittle, then, when moistened, becoming gelatinous, orange, cylindroid or tongue-shaped (5–10 mm long, 2 mm thick). – **Teliospores** 2-celled, lanceolate or fusiform, varying in size from 50–60 × 15–21 µm at margin to 100–120 × 10–12 µm in the centre, slightly constricted at septum; wall thickness 1 µm in centre of sorus to 2.5 µm at sorus margin, light brown at margin, pale yellow in centre; germ pores 2 per cell, near septum; pedicels cylindrical, very long, persistent. – **Basidiospores** with orange contents. – References: Gäumann (1959: 1153–1154), Wilson and Henderson (1966: 116), Helfer (2005: 335–336).

Remarks. Helfer (2005) lists *Sorbus aria* as host of *Gymnosporangium clavariiforme*. However, in his discussion of inoculation experiments, Gäumann (1959) states that this rust cannot infect *S. aria*. Helfer (2005) assumes that this rust is the most common species of the genus *Gymnosporangium* on non-cultivated host plants in Europe. – For records of *G. clavariiforme* in Austria see Poelt and Zwetko (1997: 65). In an old report from Tyrol (l.c. 67), aecia were recorded on *Cotoneaster integerrimus* (Magnus 1905, as *Aecidium cotoneasteris*). Unfortunately, no material is available to check its affiliation.

3 *Gymnosporangium confusum* Plowr. s.str.

Fig. 73c

Heteropsis-form:

0,I on: *Cotoneaster integerrimus*?, *Sorbus aucuparia*, (*Cotoneaster melanocarpus*? [syn. *C. niger*], *C. tomentosus*?, *Crataegus laevigata*, *C. monogyna*, *Cydonia oblonga*, *Pyracantha coccinea*, *Sorbus latifolia*, *S. torminalis*)

(0,I on: *Crataegus germanica* [syn. *Mespilus g.*], *Pyrus communis*) – less susceptible hosts

III on: *Juniperus* sp., (*J.* sect. *Juniperus* and *Sabina*)

Spermatogonia epiphyllous, subepidermal, only upper part protruding as distinct cone, about 100 µm wide and 110 µm high, at first yellowish then becoming dark brown, in the centre of leaf spots. – **Aecia** hypophyllous and caulicolous, in red spots, which are slightly thickened and become brown, at times on fruits, 1–2(–4) mm high, about 0.25 mm in diam.; peridium opening at the apex, at first tubular then fimbriate in upper half, yellowish to pale brown; peridial cells in surface view lanceolate, in lateral view rhombic, 60–90 × 18–24 µm; outer wall 1–1.5 µm thick, smooth; inner and side walls 5–7 µm thick, with elongate, obliquely and densely arranged warts and ridges. – **Aeciospores** 19–27 × 19–22 µm, globoid; wall 2–3 µm thick, light brown, finely 'verrucose' (>1.2 spines/µm^2); germ pores 6–10. – **Telia** caulicolous, on slight fusiform swellings; spore mass at first cushion-shaped and dark brown then, when moist, becoming yellow-orange-brown, gelatinous and irregularly conical or tongue-shaped. – **Teliospores** 35–45 × 20–26 µm, ellipsoid, at times narrower and longer; wall 2–3 µm thick, dark brown, at times hyaline and thinner; germ pores 2 per cell near septum; pedicels long. – References: Gäumann (1959: 1162–1163), Wilson and Henderson (1966: 117–118), Helfer (2005: 336).

Remarks. The telia of this rust, similar to the previous species, resemble those of *Gymnosporangium sabinae*, a fact which leads to its specific epithet (Helfer 2005). But its telia and teliospores are (slightly) smaller than those

of *G. sabinae*. *Gymnosporangium confusum* differs from *G. clavariiforme* by shorter and broader teliospores. The aecial host ranges of the three fungi are overlapping, but their aecia can readily be distinguished (see above).

Helfer (2005) lists *Cotoneaster integerrimus* and *C. tomentosus* as hosts for both *Gymnosporangium confusum* s.str. and *G. fusisporum*, while Gäumann (1959) emphasises that *G. confusum* f.sp. *typica* (*G. confusum* s.str.) did not infect *Cotoneaster integerrimus*. According to the latter author, *G. confusum* f.sp. *fusispora* (*G. fusisporum*) is strictly specialised in the aecial stage. It occurs on *Cotoneaster* spp., while f.sp. *typica* infects species of *Crataegus*, *Cydonia* and *Sorbus*. Lee and Kakishima (1999) characterise the aeciospore surface ornamentation of *G. confusum* as large-coronate. The basal parts of the processes ('spines') are columnar, the upper parts are divided into several long protuberances (for scanning electron micrographs of aeciospores of this type see Lee and Kakishima 1999: 115, fig. 2A–D). They found this type of ornamentation on species of the genera *Cotoneaster*, *Crataegus* (incl. *Mespilus*), *Cydonia* and *Pyrus*, but not on *Cotoneaster integerrimus*. In contrast, the aeciospore surface ornamentation of *G. fusisporum* on *C. integerrimus* is classified as minutely coronate. On this host, also *G. clavariiforme* occurs. The aeciospore surface ornamentation of this species is described as echinulate by Lee and Kakishima (l.c.).

For records of *Gymnosporangium confusum* in Austria see Poelt and Zwetko (1997: 65). In an old report from Tyrol (l.c. 67), aecia were recorded on *Cotoneaster integerrimus* (Magnus 1905, as *Aecidium cotoneasteris*). Unfortunately, no material was available to check its affiliation.

4 *Gymnosporangium cornutum* (J.F. Gmel.) Arthur s.str.

Figs 72b, 73e, 74, 75

Syn. *Gymnosporangium aucupariae-juniperinum* Kleb.; *G. juniperinum* (L.) Fr. f.sp. *aucupariae* Kleb.; *G. juniperinum* [nom. ambig.]; *G. juniperi* [nom. ambig.]; *G. amelanchieris* E. Fisch. s. Urban and Marková (2009)

Heteropsis-form:

0,I on: *Sorbus aucuparia*, (*S. chamaemespilus*, *S. domestica*, *S. hybrida*, *S. intermedia*, *S. latifolia*, *S. mougeotii*)
(0 on: *Sorbus torminalis*) – less susceptible host
III on: *Juniperus communis*, (*J. communis* subsp. *nana*)

Spermatogonia epiphyllous, subepidermal, only upper part protruding as distinct cone, about 110 µm wide and high, at first yellowish, then becoming dark brown, in the centre of large reddish or orange leaf spots. – **Aecia** hypophyllous, at times on fruits, on yellow spots later turning reddish; peridium cornute, 3–5 mm high, up to 0.5 mm wide, opening at the apex and slightly lacerate, but hardly fringed in appearence, yellowish-brown; peridial cells rhomboid in lateral view, 60–110 µm long; outer wall 2 µm thick and smooth, inner and side walls 8–12 µm thick, inner walls with somewhat elongate protuberances, side walls with short ridges, which are arranged ± densely and obliquely to the long axis of the cell. – **Aeciospores** 21–29 × 16–25 µm, globoid; wall 2–2.5 µm thick, brown, finely 'verrucose' (1.1 spines/µm²); germ pores 6–10. – **Telia** mainly caulicolous, on fusiform swellings of smaller branches, occasionally foliicolous; spore mass at first applanate or hemispherical and dark brown, then, when moist, becoming orange, gelatinous and shell-shaped. – **Teliospores** 2-celled, 30–55 × 15–24 µm, ellipsoid or often biconical; wall 1–2 µm thick, brown; germ pores covered with a prominent hyaline papilla, 1–2 per cell, in upper cell at or near the apex, in lower cell near the septum. – References: Gäumann (1959: 1170–1171), Wilson and Henderson (1966: 121), Helfer (2005: 337).

Remarks. Under his description of *Gymnosporangium juniperinum*, Gäumann (1959) discusses the confusion of the species concept of several authors for what is now accepted as *G. cornutum*. Gäumann's specification of *G. juniperinum* f.sp. *aucupariae* comes closest to the present *G. cornutum*. According to Gäumann (1959), *G. cornutum* mainly occurs on *Sorbus americana*, *S. aucuparia* and *S. hybrida* in the aecial stage. Kern (1973b) reports on the (apparently rare) occurrence of this rust on *Malus*. Helfer (2005) could not find confirmation for any occurrence on this host in Europe where *G. tremelloides* can be found on *Malus*. The telia of *G. cornutum* and *G. tremelloides* are similar in shape, but those of the latter species are larger in size. Lee and Kakishima (1999) compared the aeciospore surface ornamentation in *Gymnosporangium* with SEM. They characterise the wall ornamentations of *G. cornutum* as 'minutely coronate', with basal columns and small protuberances forming a crown on the top, whereas those of *G. tremelloides* are echinulate (Lee and Kakishima 1999: 116, fig. 3B, E).

For detailed information on the distribution of *Gymnosporangium cornutum* in Austria see Poelt and Zwetko (1997: 65).

(5) *Gymnosporangium fusisporum* E. Fisch.

Syn. *Gymnosporangium confusum* Plowr. f.sp. *fusispora* E. Fisch.

Heteropsis-form:

0,I on: *Cotoneaster integerrimus*?, (*C. melanocarpus*? [syn. *C. niger*], *C. tomentosus*)
III on: *Juniperus* sp., (*J.* sect. *Sabina*)

Spermatogonia epiphyllous, in the centre of leaf spots, subepidermal, only upper part protruding as a distinct cone, at first yellowish, then becoming dark brown. – **Aecia** foliicolous, hypophyllous, rarely caulicolous or fructicolous, up to 5 mm long, conical to cylindrical; peridium soon rupturing at apex and becoming laciniate to base; peridial cells rhomboid; walls with ridges of varying length. – **Aeciospores** 19–35 × 18–24 µm, globose or broadly ellipsoid; walls 2–3 µm thick, light brown, finely verrucose (1.2 warts/µm²); germ pores 6–9. – **Telia** caulicolous on fusiform swellings, of varying size, dark brown, swelling

Figure 74. *Gymnosporangium* cf. *cornutum* on *Sorbus aucuparia*: **a.** Spermatogonia on upper leaf side; **b.** Young aecia; no assignment to a definite species can be made before aecia are developed.

Figure 75. *Gymnosporangium cornutum* on *Sorbus aucuparia*: fully developed aecia on the lower leaf surface.

and becoming orange-brown and gelatinous when moist. – **Teliospores** 2-celled, 46–90 × 16–24 µm, fusiform, sometimes falcate; wall thickness 1.5–2.5 µm; germ pore 1 per cell, located near septum. – Reference: Helfer (2005: 337).

Remarks. Gäumann (1959) does not recognise *Gymnosporangium fusisporum* as a species of its own, but refers to it as *G. confusum* f.sp. *fusispora*. However, due to three differing characters we do not follow him. First, their telial stages (especially teliospore sizes) digress from each other and justify the differentiation (Helfer 2005). Second, the number of germ pores is clearly different. Third, despite the similarity of *G. fusisporum* and *G. confusum* in many features of the aecial stage, their spore wall ornamentation differs significantly. Lee and Kakishima (1999) characterise the aeciospore surface ornamentation of *G. fusisporum* on *C. integerrimus* as 'minutely coronate' (MC), while in *G. confusum* they state a 'large coronate' (LC) ornamentation. In both cases, the basal parts of the processes ('warts') are columnar, and the upper parts are divided into protuberances. The difference between MC and LC refers to the absolute size on the one hand, and to the degree of the length of the protuberances in comparison to the column on the other. In MC, the absolute size is usually smaller and the spikes of the crown are small, while in LC especially the spikes are much longer (Lee and Kakishima 1999: 116, fig. 3A, B, E; Helfer 2005: 332, fig. 3f).

An old record of aecia on *Cotoneaster integerrimus* from Tyrol (Magnus 1905, as *Aecidium cotoneasteris*) might belong to *Gymnosporangium fusisporum* (Poelt and Zwetko 1997: 67). Unfortunately, no material was available to check its affiliation.

6 *Gymnosporangium gaeumannii* H. Zogg (subsp. *gaeumannii*)

Life cycle insufficiently known:

II,[III] on: *Juniperus communis* subsp. *nana*?, (*J. communis* subsp. *communis*)

Spermatogonia and aecia wanting. – **Uredinia** epiphyllous on two-year-old (or older) needles, 0.5–1.5 mm long, 0.3–1 mm wide, erumpent, ± pulverulent, cinnamon-brown or blackish-brown. – **Urediniospores** borne singly on pedicels, globoid or ellipsoid, (19–)21–25(–31) × (16–)20–23(–25) µm, predominantly 1-celled, occasionally 2-celled; walls verrucose, thin (typical urediniospores) or 3–5 µm thick (amphispores); germ pores 6–8,

scattered, covered by a hyaline papilla. – **Telia** lacking. – **Teliospores** scattered in the uredinia, biconical, ellipsoid, rarely fusiform, (25–)33–46(–58) × (16–)25–33(–41) µm, 2- or 1-celled, brown; walls smooth, thin, at times thicker; germ pores 1(–2) per cell, apical or near septum; pedicels hyaline, persistent, rather long. – References: Gäumann (1959: 1151), Holm (1968: 463–465).

Remarks. *Gymnosporangium gaeumannii* produces abundant urediniospores. This character is exceptional in the genus *Gymnosporangium*. According to Holm (1968), the urediniospores of *G. gaeumannii* have a remarkable similarity to the aeciospores. Holm hypothesised that they represent a primitive type of teliospores and that the original aeciospores of rust fungi are similar to primitive teliospores. Hiratsuka (1973a) germinated spores of *G. gaeumannii* subsp. *albertense* Parmelee and observed their nuclear conditions before and after germination. His results reject the hypothesis of Holm (1968). The 1- and 2-celled, verrucose, multi-pored spores have two nuclei (per cell), and no nuclear fusion or division occurs. Therefore, these spores are urediniospores. The 1- and 2-celled, smooth, usually single-pored teliospores have one large nucleus (per cell), and nuclear division occurs. Then a 4-celled basidium and four basidiospores are produced. Except that the pedicels do not become gelatinous, the smooth spores are typical teliospores of the genus *Gymnosporangium*.

Gymnosporangium gaeumannii subsp. *gaeumannii* is described from a location in the Swiss Alps. Poelt and Zwetko (1997: 66) cite an old record from Tyrol and presume that it pertains to this characteristic rust on juniper needles.

7 *Gymnosporangium sabinae* (Dicks.) G. Winter

Figs 73b, 76, 77, 78

Syn. *Gymnosporangium fuscum* Hedw.f. in DC. [nom. illeg.]

Heteropsis-form:

0,I on: *Pyrus communis*, (*P.* ×*nivalis*, *P. pyraster*, *P. salviifolia*)

III on: *Juniperus chinensis*, *J. sabina*, (*J. virginiana*)

Spermatogonia epiphyllous, in the centre of orange leaf spots, subepidermal, only the upper part slightly protruding as a cone, 170–190 µm wide, 150–170 µm high, at first reddish, then becoming dark brown. – **Aecia** hypophyllous on reddish swellings, sometimes producing caulicolous cankers, occasionally fructicolous, 0.5–1 mm in diam., 2–5 mm high; peridia laterally bulging and splitting to the base into fibers which remain united at the apex; apex remaining bluntly conical, pale brownish; peridial cells rhomboid in surface view, 65–100 × 20–28 µm; inner and lateral walls strongly thickened, papillose, with ± separate papillae which are larger and more crowded at the upper end of the cell. – **Aeciospores** 22–29 × 25–31 µm, globoid to ellipsoid; walls 3–4.5 µm thick and dark brown, finely verrucose (1.2 warts/µm²); germ pores 6–10 (Fig. 76). – **Telia** caulicolous, usually on older, ± swollen branches, at first pulvinate and blackish brown, then, when moist,

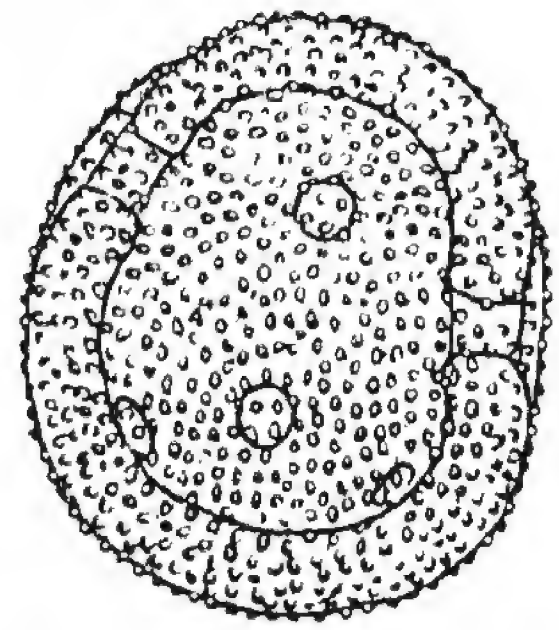


Figure 76. *Gymnosporangium sabinae*, aeciospore with distinct germ pores (from Klebahn 1914: 646).

becoming orange-brown, gelatinous, tongue-shaped, up to 1 cm wide and 2 cm high. – **Teliospores** 2-celled, 18–30 × 40–50 µm, oval to biconical, bluntly conical at the apex; wall 1–3 µm thick, nearly hyaline to dark brown; each cell with 1 germ pore near the septum; pedicels hyaline, very long. – References: Gäumann (1959: 1158–1159), Wilson and Henderson (1966: 119–120), Helfer (2005: 238–239).

Remarks. Helfer (2005) lists *Juniperus communis* in addition to other junipers as host of *Gymnosporangium sabinae*. We did not find any other record of this host-parasite combination in European literature. Blumer (1963) emphasises that *G. sabinae* cannot infect *J. communis*. In a garden near Graz, the authors of this flora observed that *J. communis* remains healthy when growing beside heavily infected *Pyrus communis* and *Juniperus chinensis* cult.

Gymnosporangium sabinae is one of the first rusts for which host alternation has been proven by artificial inoculation (Œrsted 1865). Today, the aecia on *Pyrus* trees are widely distributed; in some years the trees are heavily infected. During wet weather conditions, telia on *Juniperus* swell to large, orange, gelatinous formations, soon drying up and becoming inconspicuous brown incrustations, soon dropping off and often overlooked. Because *Juniperus sabina* is only rarely planted nowadays, it is only infrequently available as host. Therefore, we have to assume that mainly *J. chinensis* and other easily cultivated host species back up the rust cycle. Gäumann (1959) briefly discusses the potential of the rust to outlive in its haplophase. – For nomenclature, see Laundon (1975) and Braun (1982).

Gymnosporangium sabinae is widespread and common in Austria (Poelt and Zwetko 1997: 66–67). Arguably, this rust represents the economically most important parasite among the genus *Gymnosporangium* in Europe. It is extremely widespread where the corresponding hosts live together (Helfer 2005).

Gymnosporangium asiaticum Miyabe ex Yamada has been found in Europe on bonsai *Juniperus chinensis* imported from Japan (Henderson and Bennell 1979). This rust is a serious pathogen of *Pyrus pyrifolia* (Japanese pear) and *Juniperus chinensis* in E Asia. European pear (*Pyrus communis*) and quince (*Cydonia oblonga*) are recorded as hosts, too. But the study of Sakuma (1992) shows that European pear is only slightly susceptible.

Figure 77. *Gymnosporangium sabinae*, mostly on *Pyrus communis*: **a.** Spermatogonia in orange leaf spots on the upper leaf surface; at this stage, no swellings of the leaf tissue and no aecia are visible yet; **b.** Aecia on gall-like swellings on the lower leaf surface (on *Pyrus pyraster*); **c.** Old aecia; **d.** Two aecia at higher magnification; note that the peridium is regularly ruptured into fine fibres but its apex remains intact, also after spore release; (**b** by Julia Kruse; **d** by Walter Obermayer).

Figure 78. *Gymnosporangium sabinae* on *Juniperus* sp.: **a.** Telia as tongue-shaped gelatinous excrescences developed after rain; **b.** Telia appearing as hard incrustations after drying up; (**a** from Zwetko 2000: front cover).

(8) *Gymnosporangium torminali-juniperini* E. Fisch. ex F. Kern

Syn. *Gymnosporangium juniperinum* (L.) Fr. f.sp. *torminali-juniperinum* E. Fisch. s. Gäumann (1959); *G. amelanchieris* E. Fisch. s. Urban and Marková (2009); *G. torminali-juniperinum* E. Fisch. ex F. Kern (orthogr. var.)

Heteropsis-form:

(0,I on: *Sorbus latifolia*, *S. torminalis*)

(III on: *Juniperus communis*)

Spermatogonia epiphyllous, subepidermal, only the upper part protruding as a distinct cone, first yellowish, then becoming dark brown, in the centre of leaf discolourations. – **Aecia** hypophyllous, 2–5 mm high, 0.3–0.4 mm wide; peridium opening at apex, becoming ± split along the sides; peridial cells rhomboid in lateral view, 65–100 µm long; outer wall 2–3 µm thick, smooth, inner and side walls 6–7 µm thick, densely covered with elongate papillae and fine ridges of varying length. – **Aeciospores** 24–27 × 18–24 µm, broadly ellipsoid; wall 1.5–2.5 µm thick, cinnamon-brown, finely verrucose (1.1 warts/µm^2); germ pores 6–10. – **Telia** foliicolous, predominantly epiphyllous, 1–2 mm long, 0.5–1.5 mm high, hemispherical, brown, when moist becoming gelatinous. – **Teliospores** 2-celled, 35–49 × 21–30 µm, broadly ellipsoid; wall 1–1.5 µm thick, pale brown; germ pores 1–2 at the apex or near the septum; hyaline papilla on apex 3–6 µm high; pedicels hyaline and rather long. – Reference: Helfer (2005: 339).

Remarks. After carrying out a number of inoculation experiments, Fischer (1910) distinguishes three *Gymnosporangium* species which produce cornute aecia, *G. amelanchieris*, *G. cornutum*, and *G. torminali-juniperini*. The results of his experiments show that *G. torminali-juniperini* does not infect the aecial hosts of the two other species. However, Helfer (2005) lists several *Sorbus* species as hosts of *G. torminali-juniperini* (e.g., *S. aucuparia*, *S. chamaemespilus*, *S. domestica*, *S. hybrida*, *S. latifolia*, *S. mougeotii*, *S. torminalis*). With the exception of *S. latifolia* and *S. torminalis*, we did not find any other record of those host-parasite combinations in European literature. *Gymnosporangium torminali-juniperini* is morphologically similar to *G. cornutum* and *G. amelanchieris*. These rusts with cornute aecia are regarded as a collective species made up of a number of races or special forms (Gäumann 1959; Majewski 1977; Urban and Marková 2009). Nevertheless, they show morphological differences, which justify separation (Fischer 1910; Sydow and Sydow 1915; Helfer 2005). The peridial cells of aecia of *G. amelanchieris* and *G. cornutum* are covered with less minute and less densely arranged ridges than those of *G. torminali-juniperini*. The teliospores of *G. torminali-juniperini* have higher papillae over the germ pores than those of the two other species. – According to Poelt and Zwetko (1997: 67), *G. torminali-juniperini* is reported from South Tyrol (Italy).

9 *Gymnosporangium tremelloides* R. Hartig

Figs 72a, 73d, 79

Syn. *Podisoma tremelloides* A. Braun; *Gymnosporangium ariae-tremelloides* Kleb.; *G. penicillatum* Liro

Heteropsis-form:

0,I on: *Malus domestica*, *Sorbus aria*, *S. chamaemespilus*, (*Cydonia oblonga*, *Malus baccata*, *M. sylvestris*, *Sorbus aucuparia*, *S. hybrida*, *S. latifolia*, *S. torminalis*)

III on: *Juniperus communis*, *J. communis* subsp. *nana*

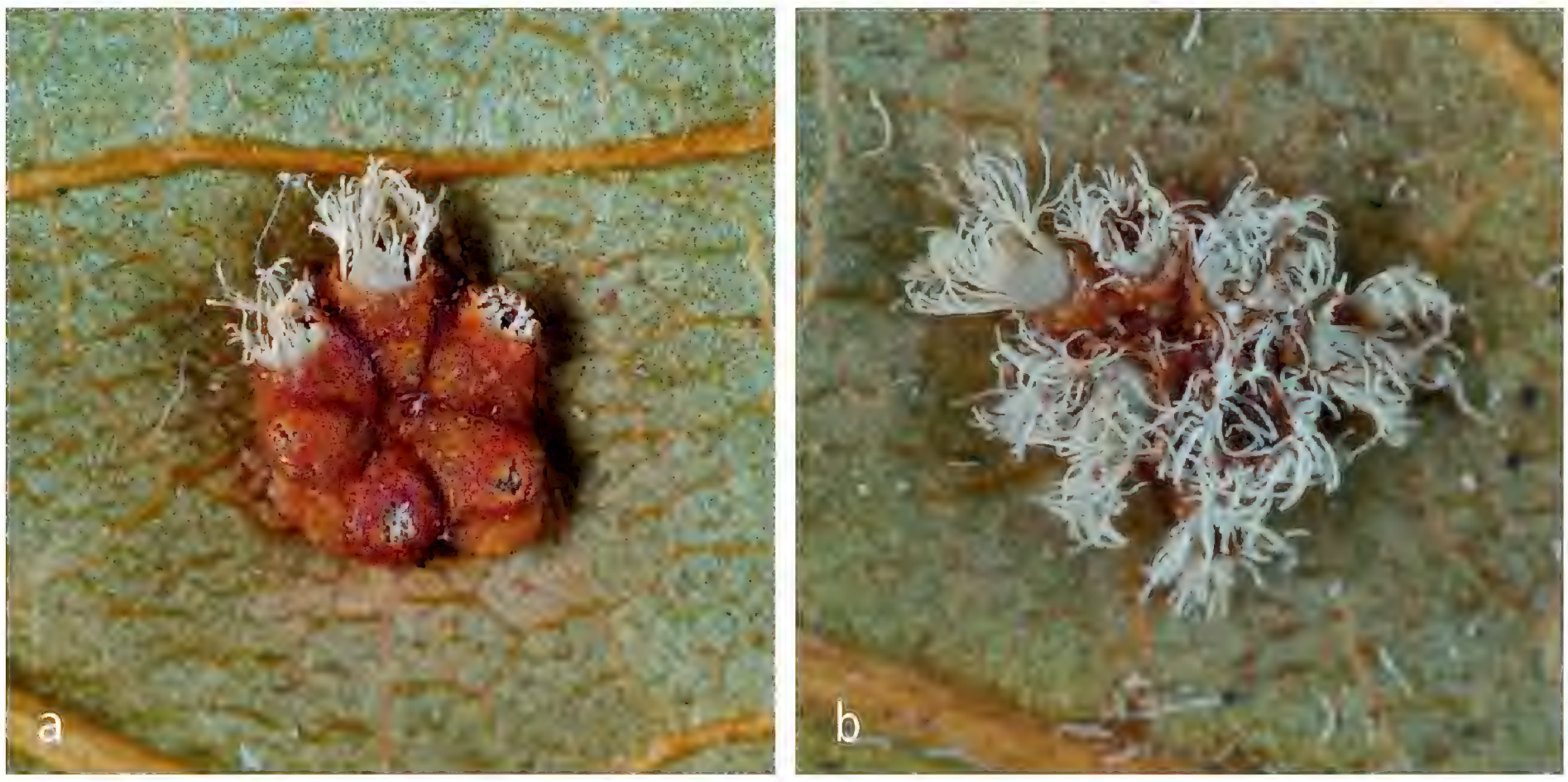


Figure 79. *Gymnosporangium tremelloides* on *Sorbus chamaemespilus*: **a.** Reddish-brown leaf gall with young aecia; **b.** Aecia with fully developed white peridia.

Spermatogonia epiphyllous, subepidermal, only upper part protruding as distinct cone, 150 µm wide, 170 µm high, at first yellowish, then becoming dark brown; in the centre of leaf discolourations. – **Aecia** hypophyllous, on yellow, later red or reddish-brown swellings; peridium 0.5–1.5(–3) mm high, at first cylindrical, but soon becoming fimbriate to the base, white; peridial cells rhomboid in section view, 60–90 × 31–35 µm; inner and lateral walls thickened, covered with elongate and rather wide, obliquely arranged ridges which do not extend to the outer margin. – **Aeciospores** rather large, 30–50 × 25–35 µm, very variable, globoid-ellipsoid; walls 3–5 µm thick, dark brown, finely verrucose (>1.2 warts/µm²); germ pores 6–8, dispersed. – **Telia** caulicolous on fusiform galls (up to 5 mm wide, up to 20 mm long and 1–2 mm high), also on needles (smaller than on galls), brown and applanate when dry, orange(-brown), gelatinous and shell-shaped when moist. – **Teliospores** 2-celled, 35–70 × 20–30 µm, ellipsoid to bluntly biconical; wall 1–2.5 µm thick, light brown to dark brown, smooth; lower cell with 2 germ pores near septum, upper cell with 2–3 germ pores (1–2 near the septum, 1 at apex). – References: Gäumann (1959: 1166–1167), Helfer (2005: 339–340).

Remarks. *Gymnosporangium tremelloides* is reported to show a number of specialised forms. According to the results of inoculation experiments summarised by Gäumann (1959), f.sp. *ariae-tremelloides* Kleb. can infect several *Sorbus* species (e.g., *Sorbus aria*, *S. aucuparia*, *S. chamaemespilus*, *S. hybrida*, *S. latifolia*, *S. torminalis*) and produces spermatogonia and aecia on them. If *Malus* is inoculated, only spermatogonia are produced. In contrast, f.sp. *mali-tremelloides* Kleb. infects *Malus* species and produces both, spermatogonia and aecia.

According to Kern (1973a), this rust has caused taxonomic confusion, and knowledge on its distribution should be improved as well. However, its exceptionally large aeciospores provide a clear character for identification (Helfer 2005).

For records of *Gymnosporangium tremelloides* in Austria see Poelt and Zwetko (1997: 67). In this country, collections of *G. tremelloides* on *Malus domestica* are rather rare because the telial host does not occur on many sites where apple trees are cultivated. Therefore, this rust is of minor importance in apple plantations.

In N America, the cedar apple rust *Gymnosporangium juniperi-virginianae* Schwein. (Fig. 80) causes a serious disease on apple trees. The telial host is *Juniperus virginiana*. This host plant is cultivated as an ornamental tree or shrub in gardens, sometimes in close vicinity to apple trees in Europe as well. In Great Britain, *G. juniperi-virginianae* has been recorded occasionally on imported apples (Wilson and Henderson 1966: 122).

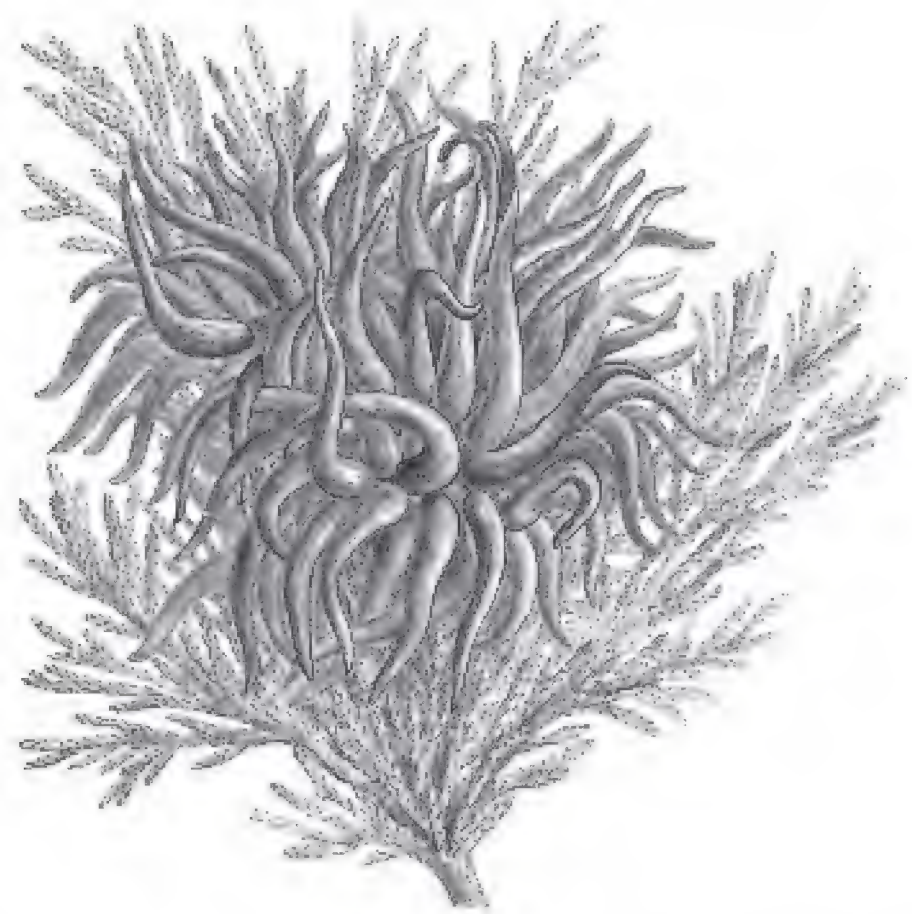


Figure 80. *Gymnosporangium juniperi-virginianae* on *Juniperus virginiana*: gelatinous telia (in nature of bright orange colour) on branches of its host which is often cultivated as an ornamental plant in our region (from Dietel 1928: 76, with permission from Duncker & Humblot GmbH).

Ochropsoraceae Aime & McTaggart

The following brief description and comment are cited from Aime and McTaggart (2020: 35): "Spermogonia

Group VI (type 7). Aecia aecidium-type; uredinia malupa-type; aecial states systemic, overwintering as mycelium; telia [basidiosori] forming crusts, 1-cell deep, at first subepidermal, then erumpent; teliospores [basidia] germinate without dormancy, either internally (*Ochropsora*) or externally (*Aplopsora*). Species likely macrocyclic and heteroecious, although gametothallus not known for *Aplopsora*." … "A monophyletic Ochropsoraceae as the earliest diverging lineage of [suborder] Raveneliineae was recovered in all of our analyses."

Ochropsora Dietel

The small genus with uredinia and telia on Rosaceae and aecia on Ranunculaceae is represented only by the type species in Europe. Ono (2006) studied basidium morphology of *Ochropsora anemones* (syn. *O. ariae*). The rust produces 1-celled probasidia in a single horizontal layer beneath the host epidermis. The apical portion of the probasidium elongates to turn into a 4-celled metabasidium. The basidiosori (telia) of the fungus seem to become naked quickly as they mature; germination occurs without dormancy. Bauer and Oberwinkler (1986) investigated the development of basidia and the germination of basidiospores of *O. anemones*. They found that this rust develops 'gastroid' basidia in host tissues and on artificial media. It forms no curved sterigmata and the basidiospores are not actively discharged. The authors assume that the evolution of 'gastroid' form and function of these basidia is due to enclosure of mature spores in the host tissue. Cummins and Hiratsuka (2003) and Ono (2006) placed *Ochropsora* in the family Chaconiaceae.

This family is presumed to be basal in the phylogeny of the rust fungi. However, most species of chaconiaceous genera are distributed in the tropical or subtropical regions, while *Ochropsora* is restricted to temperate regions. Molecular data support sister group status of *Ochropsora* and *Tranzschelia* (Maier et al. 2003). Therefore, we keep it separate from Chaconiaceae. See also the more recent family description and comment cited above.

1 *Ochropsora anemones* (Pers.) Ferd. & C.A. Jørg.

Figs 81, 82

Syn. *Ochropsora ariae* (Fuckel) Ramsb.; *O. sorbi* (Oudem.) Dietel

Hetereu-form:

0,I on: *Anemone nemorosa*, *A. ranunculoides*, *A. trifolia*

II,III* on: *Aruncus dioicus*, *Prunus padus*, *Sorbus aucuparia*, *S. torminalis*, (*Amelanchier asiatica*, *Malus domestica*, *M. sylvestris*, *Prunus avium*, *P. tenella*, *Pyrus communis*, *Sorbus aria*, *S. intermedia*, *S. latifolia*)

Spermatogonia on both sides of the leaf, but mostly on the upper side, scattered, subcuticular, sitting on epidermis, first whitish then brownish. – **Aecia** hypophyllous, 0.4 mm in diam., arising from a systemic mycelium, ± covering the whole lower leaf surface, subepidermal, erumpent, cupulate, with a broad revolute peridium divided into a few broad lobes; spore mass whitish to (golden-)yellowish. Infected shoots stand erect, are usually paler and have smaller lobes; the stems are longer; affected plants do not flower, or develop imperfect flowers. – **Aeciospores** produced in chains, 17–26 × 16–21 µm; wall 1 µm thick (or less), subhyaline to (golden-)yellowish, finely, densely and evenly verrucose; germ pores obscure; contents hyaline. – **Uredinia** hypophyllous, 0.1–0.3 mm in diam., subepidermal, erumpent, in chlorotic leaf spots, small, scattered or in groups, whitish to yellowish, surrounded by clavate or incurved paraphyses which are joined at the bottom and form circular cups; paraphyses c. 60 µm long, 14–18 µm wide. – **Urediniospores** borne singly on pedicels, 19–28 × 15–25 µm; wall hyaline or very pale brownish, evenly 1–1.5 µm thick, evenly echinulate; spine distance 1.5 µm; germ pores indistinct. – **Basidiosori** (telia) hypophyllous, 0.3–0.5 mm in diam., subepidermal, in small, circular crusts, pale pink, waxy in appearence, becoming erumpent. – (Meta-) **Basidia** (teliospores) sessile, at first 1-celled, later on dividing into four cells, 30–70 × 10–18 µm; wall 1 µm thick, hyaline, smooth; contents opaque grey. – References: Gäumann (1959: 1216–1219), Helfer (2005: 342), Ono (2006: 147–148).

Remarks. Like in *Tranzschelia*, the mycelium of the aecial stage is perennial in the rhizome of *Anemone*. Records on *Anemone ranunculoides* are very rare. *Ochropsora anemones* has been reported on this host from Austria (near Vienna) by Speer (1971) and from Russia (near Moscow) by Kursanov (1922). Distinguishing features for aecia of *Tranzschelia pruni-spinosae* and *O. anemones* are colour of spore mass, as well as colour and thickness of spore wall (see also under *T. pruni-spinosae*). The uredinia of *Ochropsora* differ from those of *Tranzschelia* and *Leucotelium* by the presence of abundant peripheral paraphyses, which form circular cups. The urediniospores of *Ochropsora* have evenly thin and evenly echinulate spore walls. In *Tranzschelia* the urediniospores bear the spines at the sides but at the apex they are smooth and the spore wall is thickened there.

It is remarkable that this rust has not been found on the commonly cultivated *Prunus avium* (cherry) in Central Europe. In Austria *Ochropsora anemones* occurs frequently on moist and shady sites (gorges, ravine forests and canyons). In the dikaryophase, young trees or the lowest branches or *Aruncus*, respectively, in the understorey become infected (Poelt and Zwetko 1997: 91–92).

A key for all rust genera and species with uredinia and telia on *Prunus* is attached to *Leucotelium cerasi* (p. 312).

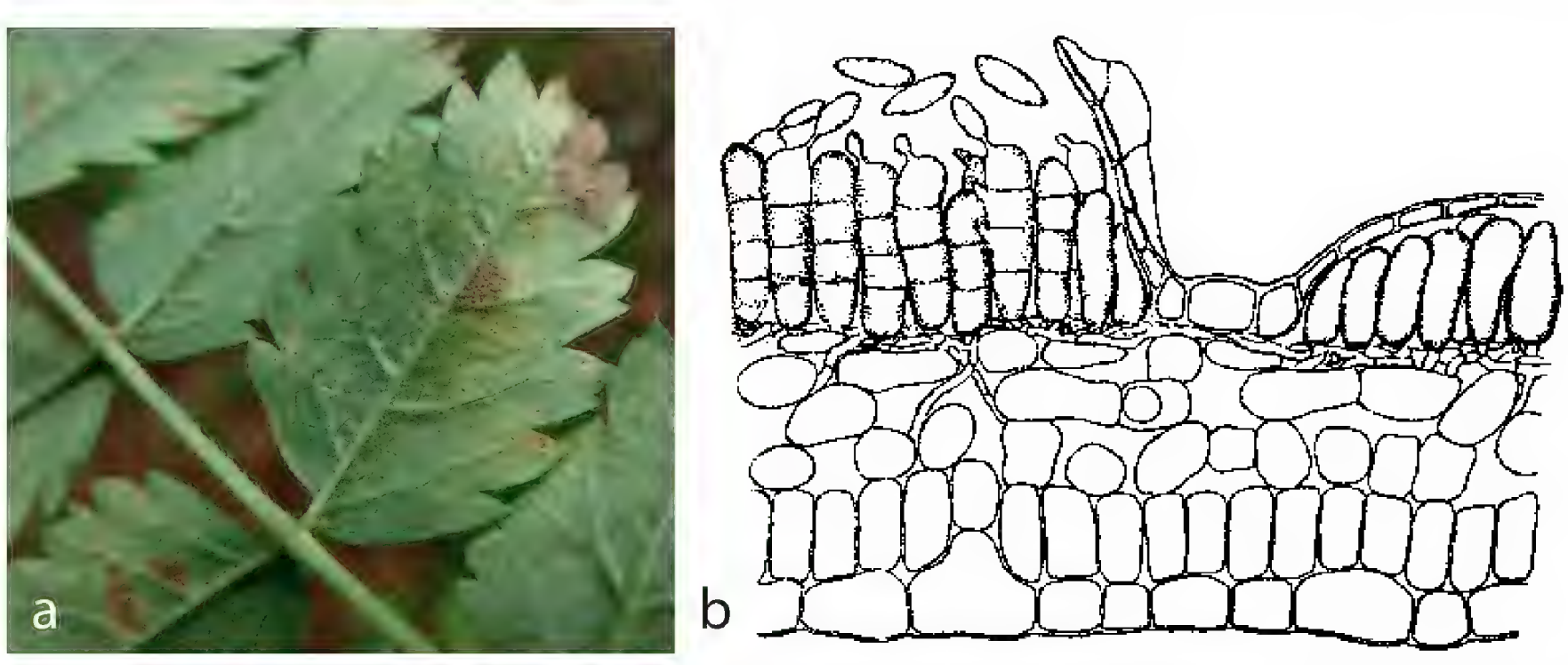


Figure 81. *Ochropsora anemones*. **a.** Young basidiosori (telia) on *Sorbus aucuparia*; **b.** Basidiosori in vertical section; basidia on the right side are young and 1-celled, on the left fully developed and 4-celled, together with basidiospores; (**a** by Julia Kruse; **b** from Dietel 1928: 55, with permission from Duncker & Humblot GmbH).

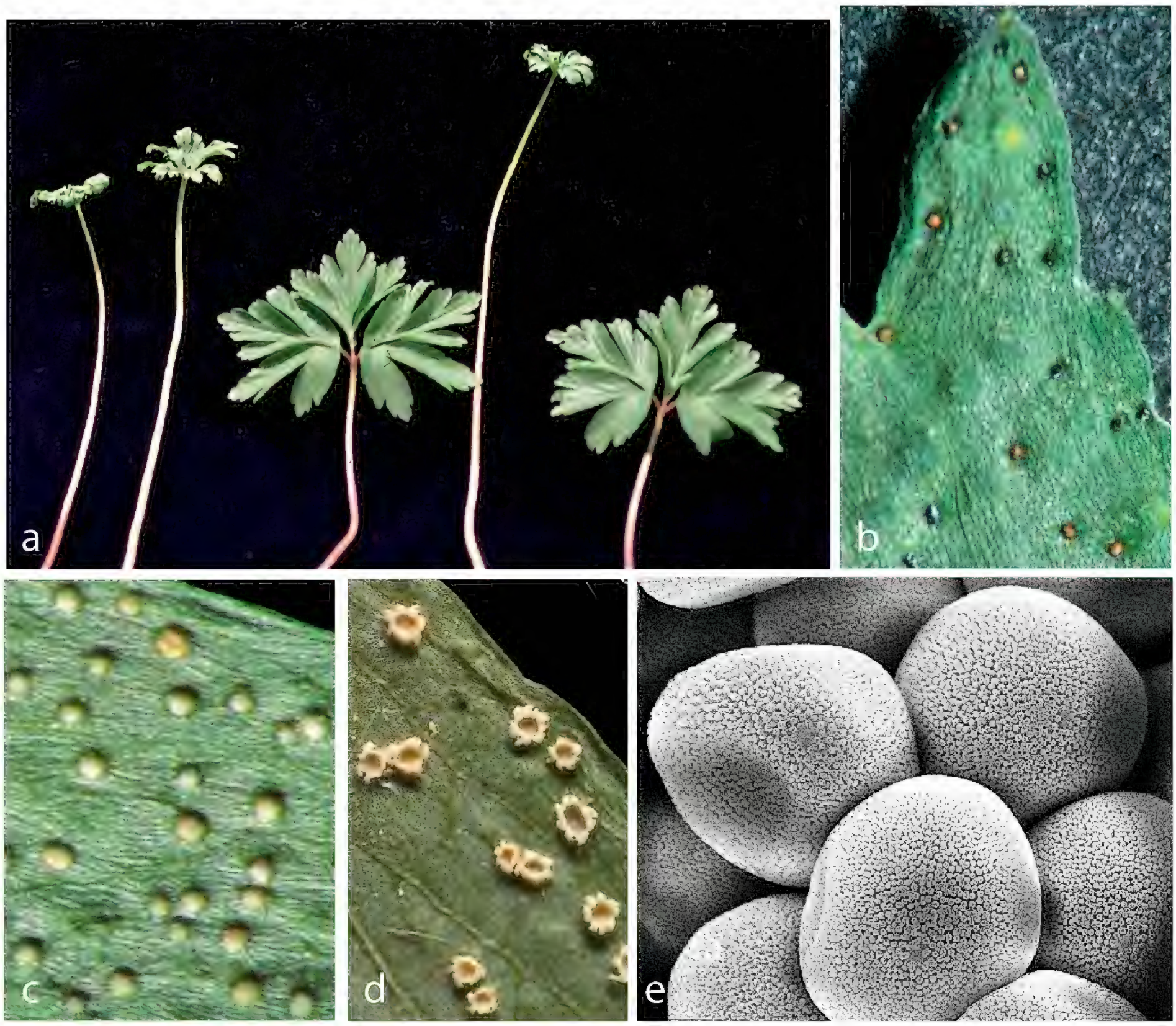


Figure 82. *Ochropsora anemones* on *Anemone nemorosa*: **a.** Three infected shoots/leaves with smaller leaf segments and taller stem/petiole, and two uninfected leaves with shorter petiole; **b.** Epiphyllous spermatogonia; **c.** Hypophyllous young aecia; **d.** Fully developed aecia with curved lobes of the white peridia and pale yellowish spore mass; **e.** Aeciospores showing evenly verrucose ornamentation in SEM; (**e** by Paul Blanz).

Phragmidiaceae Corda

The family Phragmidiaceae is characterised by its restriction to Rosaceae (Rosoideae) as hosts. All European Phragmidiaceae have an autoecious life cycle. According to Cummins and Hiratsuka (2003), their spermatogonia fit group IV (types 6, 8, 10 and 11). Besides *Phragmidium*, *Kuehneola* and *Xenodochus*, Savile (1989) and Poelt and Zwetko (1997) also include *Triphragmium* due to its hosts and its autoecious life cycle. This assignment is supported by Maier et al. (2003) and Aime (2006) on the basis of molecular data. In contrast, Cummins and Hiratsuka (2003) assign this genus to the Raveneliaceae due to its spermatogonia group VI, type 7. Also on sequence data, Yun et al. (2011) favour a separate position of *Gymnoconia* and *Trachyspora* within the Phragmidiaceae.

Gymnoconia Lagerh.

Syn. *Arthuriomyces* Cummins & Y. Hirats.

The small genus which is predominantly distributed in N America attacks various *Rubus* species. It holds several taxa which develop either as autopsis-form, or according to the *Endophyllum* mode (endo-form). In this mode, teliospores are reduced, and the morphological aeciospores germinate with basidia.

Taxonomy and nomenclature of *Gymnoconia* are questionable. Laundon (1975) restricted this name to the endocyclic taxa occurring spontaneously in N America, and Cummins and Hiratsuka (1983) subsequently introduced the monotypic genus *Arthuriomyces* for the autopsis-form treated below. But Laundon's argument was flawed by Cummins and Hiratsuka (2003; compare

Vogler and Bruns 1993 with respect to *Cronartium* und '*Endocronartium*'). It is always doubtful if a reduced life cycle justifies the establishment of a separate genus, especially since the different life cycles are apparently not fixed in *Gymnoconia*. According to Gäumann (1959), 'macrocyclic' and 'microcyclic' aeciospores occur in the very same sorus, i.e., these spores develop either in the autopsis mode or in the *Endophyllum* mode; in a preliminary way, Gäumann combines macrocyclic and microcyclic forms in one species.

According to its host range and morphology, the genus *Gymnoconia* fits the Phragmidiaceae. However, based on differences in number of cells of the teliospores and form of basidiospores as well as presence of paraphyses in the caeomoid aecia, Dietel (1928) keeps the tribus Gymnoconieae with the genera *Gymnoconia* and *Trachyspora* separate from the tribus Phragmidieae. This is reflected by molecular data published by Yun et al. (2011) which indicate a separate position of these two genera within the Phragmidiaceae. For an unambiguous assignment of *Gymnoconia* to this family, more molecular genetic data would be helpful.

For keys to the rusts on *Rubus* see under *Phragmidium violaceum* (p. 305).

(1) *Gymnoconia peckiana* (Howe) Trotter

Fig. 83

Syn. *Arthuriomyces peckianus* (Howe) Cummins & Y. Hirats.; ?*Gymnoconia interstitialis* (Schltdl.) Lagerh.; *G. nitens* auct. (see remarks)

Autopsis-form:

(0,I,III on: *Rubus saxatilis*)

Spermatogonia on both sides of the leaf, subcuticular, protruding cone shaped, up to 75 µm high. – **Aecia** caeomoid, produced by a systemic mycelium, usually covering the whole lower surface of the leaf, subepidermal in origin, erumpent, 0.5–1.5 mm, orange when fresh. – **Aeciospores** 19–38 × 16–34 µm, ellipsoid; wall 1.5–2 µm thick, hyaline, finely verrucose; distance of warts about 1 µm; germ pores indistinct; contents orange. – **Telia** hypophyllous on yellow spots, scattered, not confluent, not produced by a systemic mycelium, small (0.3 mm), dark brown, partly covered by the epidermis. – **Teliospores** 30–50 × 18–30 µm, 2-celled, polymorphic, very slightly constricted at the septum; wall thin (1–1.5 µm), not thickened at the apex, with 1 germ pore in each cell, often with 1–6 small, hyaline papillae around the pores; pore of the upper cell in apical position; pore of the lower cell often on a somewhat conical or tapering protrusion; pedicels hyaline, not persistent. – References: Gäumann (1959: 209), Helfer (2005: 333, 334).

Remarks. In N Europe, this autopsis-form is rather widely distributed, soon becoming rare towards the South. However, *Gymnoconia peckiana* is well known from Switzerland and S Bavaria but has not been reported from Austria so far (Poelt and Zwetko 1997: 63, as *Gymnoconia nitens*).

The name *Gymnoconia nitens* (Schwein.) F. Kern & Thurston [syn. *Kunkelia nitens* (Schwein.) Arthur; *Caeoma nitens* (Schwein.) Newcombe] s. Cummins & Hiratsuka refers to microcyclic forms found only in N America. The name 'orange rust' is used either for the microcyclic forms or for the aecial stage of the macrocyclic form.

Kuehneola Magnus

All species are autoecious; most are on Rosaceae. *Kuehneola* differs from *Phragmidium* by the number of germ pores in each teliospore cell (1 instead of 2 or more) and the lack of paraphyses in the uredinia. In Central Europe, the small genus is represented by the type species only.

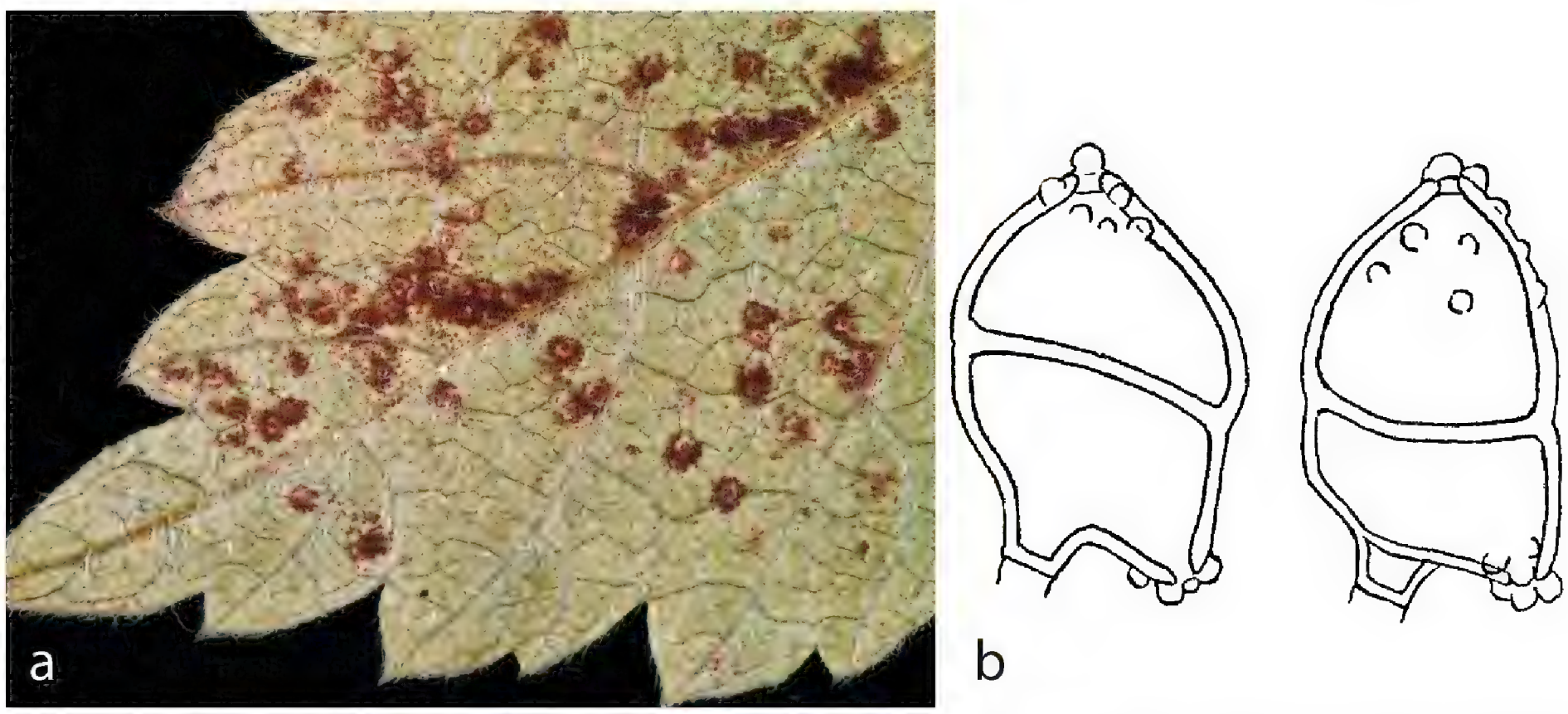


Figure 83. *Gymnoconia peckiana* on *Rubus saxatilis*: **a.** Telia on the lower leaf side; herbarium material does not show the leaf spots around the sori visible in fresh samples; **b.** Teliospores with papillae around the germ pores; (**b** from Klebahn 1914: 666).

1 *Kuehneola uredinis* (Link) Arthur

Figs 84, 85

Syn. *Kuehneola albida* (J.G. Kühn) Magnus

Brachy-form:

0,IIa+b,III on: *Rubus bifrons*, *R. clusii* [as *R.* '*gremlii*'], *R. constrictus* [syn. *R. vestii*], *R. ferox*, *R. laciniatus* cult., *R. pedemontanus* [syn. *R. bellardii* p.p.], *R.* sect. *Rubus*, *R. salzmannii*, *R. styriacus*, *R. widderi*, (*R. caesius*?, *R. canescens*, *R.* sect. *Corylifolii*, *R. fuscus*, *R. gracilis*, *R. hirtus*, *R. macrophyllus*, *R. montanus*, *R. plicatus*, *R. radula*, *R. rudis*, *R. sprengelii*, *R. vestitus*)

Spermatogonia epiphyllous, subcuticular, on reddish spots, large, pustular, 150–200 µm in diam., 100 µm high. – **Primary uredinia** mostly epiphyllous, surrounding the spermatogonia, small (0.5 mm), irregularly elongated and often confluent into circles, subepidermal in origin, erumpent, orange-yellow; peridium and paraphyses lacking. – **Primary urediniospores** borne singly on pedicels, globoid to obovoid, 18–29 × 16–23 µm (after Gäumann 1959 and Helfer 2005), 19–23 × 18–20 µm (after Wilson and Henderson 1966 and Petrova and Denchev 2004); wall about 2 µm thick, hyaline, finely verrucose(-echinulate); germ pores obscure; contents yellow. – **Secondary uredinia** hypophyllous and also on petioles and stems, scattered on pale golden-yellow spots, pulverulent, on the leaf minute (about 0.1 mm in diam.), often covering the whole leaf surface, soon naked, surrounded by the ruptured epidermis, on the stem subcortical, linear to irregularly elongated, up to 10 mm long and 1–1.5 mm wide, opening by a longitudinal rupture; spore mass lemon-yellow to orange; paraphyses lacking. – **Secondary urediniospores** borne singly on pedicels, obovoid, rarely globoid, 18–29 × 16–23 µm; wall 1.5–2(–2.5) µm thick, nearly hyaline, finely and closely verrucose-echinulate; germ pores indistinct, probably 3–4, equatorial. – **Telia** hypophyllous, singular or in roundish groups but never confluent, 0.1–0.5 mm in diam.; subepidermal in origin, soon erumpent, pulvinate, yellowish or whitish. – **Teliospores** in clavate or elongate-cuneate chains, which are straight or slightly curved, 40–120 µm long, composed of 2–12 (mostly 5–7) spores (after Gäumann 1959, Wilson and Henderson 1966, and Helfer 2005). – According to Petrova and Denchev (2004), each chain is composed of 2–5 (mean 3.1±0.8) spores; single teliospores obtusely cuneate or ovoid-ellipsoid, often trapezoid, 17–30 × 15–24 µm (but sometimes wider than long); walls hyaline, smooth, up to 5.5 µm thick at the top of the terminal spore; the lower transverse walls always thin and the upper thicker with irregular undulations or projections; the side walls becoming thicker from below upwards; germ pore 1 in each spore; pore of the terminal spore ± apical; pores of the other spores on short lateral projections close to the upper transverse wall; germination occurs without dormancy; each chain has a short and thin-walled basal cell (pedicel). – References: Gäumann (1959: 197–198), Wilson and Henderson (1966: 108), Petrova and Denchev (2004: 97), Helfer (2005: 340–341).

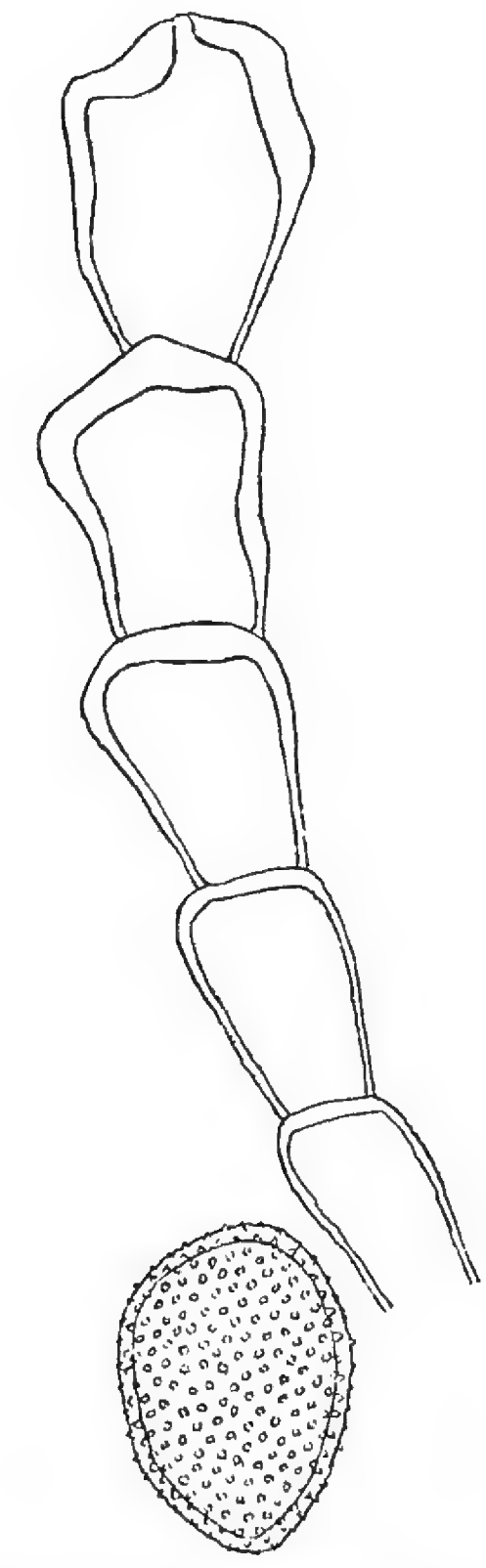


Figure 84. *Kuehneola uredinis* on *Rubus plicatus*: urediniospore and chain of teliospores (from Klebahn 1914: 692, as *K. albida*).

Remarks. Arthur (1934) and Cummins and Hiratsuka (2003) take each teliospore chain as a more-celled teliospore, which is borne singly on a short pedicel.

Gäumann (1959) has listed *Rubus caesius* as host of *Kuehneola uredinis*, but it appears to be an error (Wilson and Henderson 1966). Petrova and Denchev (2004) treated Bulgarian records of *Kuehneola uredinis* on *R. caesius* as uncertain rust-host combinations. It still has to be proven if *R. caesius* hosts this parasite. According to Gäumann (1959), *K. uredinis* can infect *Rubus* species which belong to the '*R. Corylifolii* group'. Helfer (2005) has reported *R. canescens* as host. Cummins and Hiratsuka (2003) noticed that *K. uredinis* may cause defoliation of commercial raspberry plants (*Rubus idaeus*) and can also infect stems, but this host species is not listed by Gäumann (1959) and Helfer (2005).

Frequent appearance of this rust on cultivated *R. fruticosus* agg., also in deep crevices in the stems, have been observed in Austria. These deep crevices in the stems are caused by the rust and contain secondary urediniospores. They occur in this region in spring as well as in late summer

Figure 85. *Kuehneola uredinis*. **a.** Spermatogonia and primary uredinia on the upper leaf side of *Rubus* cf. *bifrons*; **b, c.** Secondary uredinia on *Rubus fruticosus* cult.: **b.** On the lower side of an overwintered leaf collected in early spring; **c.** In deep crevices in the stem; **d.** Secondary uredinia (yellow) and numerous telia (white) on *Rubus* sect. *Rubus*; (**d** by Julia Kruse).

and in fall (Poelt and Zwetko 1997). The life cycle of this rust seems to be variable. Gäumann (1959) and other authors state that primary uredinia are produced in summer or late summer, the secondary uredinia, however, in the following spring. In turn, Klebahn (1914) reports on secondary uredinia in Brandenburg, which were found only in fall. Around Graz, primary uredinia on native *R. fruticosus* agg. are found frequently in fall. In some gardens in this area, no primary uredinia have been observed on cultivated *R. fruticosus* agg. but heavy infections with secondary uredinia instead from early spring to late autumn. – For records of *Kuehneola uredinis* in Austria see Poelt and Zwetko (1997: 69).

For keys to the rusts on *Rubus* see under *Phragmidium violaceum* (p. 305).

Phragmidium Link

Syn. *Aregma* Fr.; *Frommea* Arthur; *Frommeëlla* Cummins & Y. Hirats.; *Lecythea* Lév.; *Caeoma* auct.

The autoecious genus *Phragmidium* occurs on Rosaceae and causes a high number of diseases (Helfer 2005). It is widely distributed in N America. With 17 species, it is also the most diverse rust genus on Rosaceae in Europe. In our area, most species inhabit the planar and colline zones; some occur in mountain forests. Host genera are *Potentilla*, *Rosa*, *Rubus* and *Sanguisorba*.

– **Spermatogonia** intraepidermal (type 10 according to Cummins and Hiratsuka 2003) or subcuticular (type 11), conical or flattened. – **Aecia** caeomoid, subepidermal in origin, erumpent, orange or yellow, without peridium, usually surrounded by incurved paraphyses. – **Aeciospores** catenulate; wall hyaline, verrucose, echinulate or irregularly slab-shaped, with numerous, scattered germ pores. – Scanning electron micrographs of wall ornamentation were published by Holm et al. (1970), Bedlan (1984), and Wahyuno et al. (2002). – **Uredinia** subepidermal in origin, erumpent, orange or yellow, without peridium, usually surrounded by paraphyses. – **Urediniospores** borne singly on pedicels; wall echinulate or verrucose, often with numerous, scattered, obscure germ pores. In a few species, the germ pores are conspicuous because the pore wall forms a hemispherical projection into the lumen of the spore. – **Telia** subepidermal in origin, erumpent, brownish, cinnamon-brown or mostly black. – **Teliospores** borne singly on pedicels, often rather large, 2- to several-celled by transverse septa; wall pigmented, often obviously bilaminate, smooth or more often covered with warts and papillae; germ pores 1 or mostly 3 in each cell; pedicel often rather long and hygroscopic (swelling) in the lower half; basidia external.

Due to the unfortunate typification of *Uredo obtusa*, the name *Frommea* Arthur became a synonym of *Phragmidium* Link. Therefore, Cummins and Hiratsuka (1983) introduced the new name *Frommeëlla*. In Europe, this

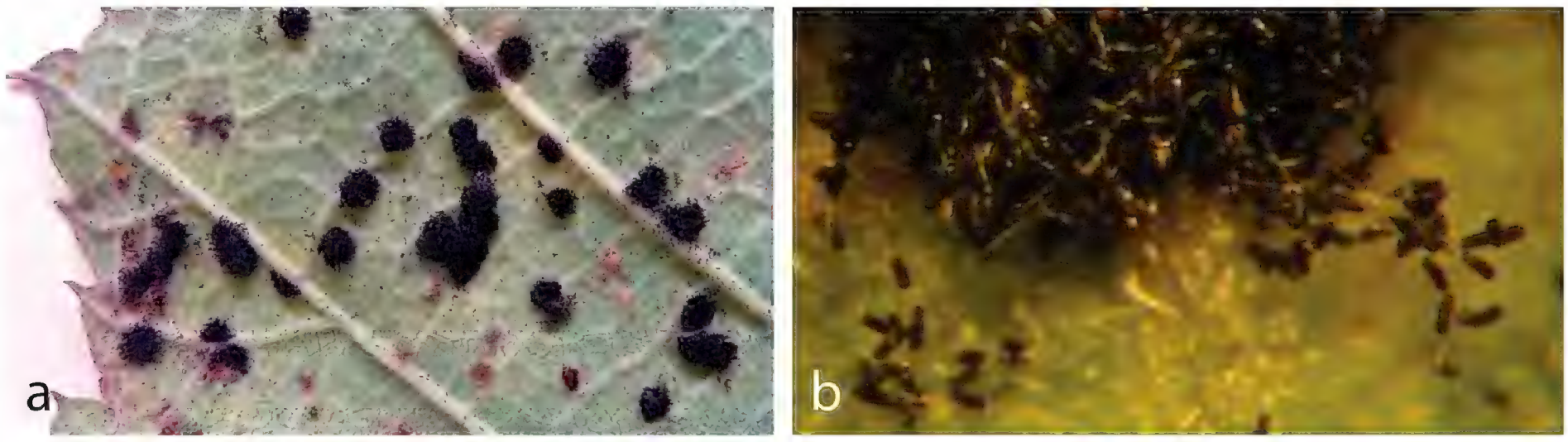


Figure 86. *Phragmidium violaceum* on *Rubus bifrons*: **a.** Telia on the lower leaf side; **b.** Part of a telium with detached and deranged spores. Teliospores with pedicels are rather large and visible with a hand lens.

small, autoecious genus is represented by one native and one introduced species. Its teliospores have only one germ pore per cell and germinate without dormancy, while the teliospores of most *Phragmidium* species have two or three and germinate after overwintering. But analyses of rDNA sequences show that species formerly placed in *Frommeëlla* belong to the genus *Phragmidium*. Therefore, *Frommeëlla* has been considered to be a generic synonym of *Phragmidium* (Yun et al. 2011).

Also the separation of *Phragmidium* into two sections by Arthur (1934) has not been confirmed by the analyses of Yun et al. (2011). Neither section *Earlea* with ± smooth teliospores borne on non-hygroscopic pedicels, nor section *Euphragmidium* with verrucose teliospores and hygroscopic pedicels form natural groupings.

Dietel (1905) describes a distinct mechanism of spore detachment in the telia of species with hygroscopic pedicels: The teliospores contain water in the lower, broadened part of their pedicels. When mature, part of this water is lost causing the pedicels to shorten and twist. Due to their verrucose surface, the spores are jammed in the sorus; this prevents them from turning together with their twisting pedicels. Therefore, the twisting pedicels become detached at their base, causing a derangement of the spore mass in the telia (Fig. 86).

The similarity of aecia and uredinia is another particular feature at least within the Central European *Phragmidium* species. The occurrence of echinulate aeciospores is special as well. Wahyuno et al. (2002) described five different types of echinulate aeciospores on roses, and Bedlan (1984) observed two of them on roses in Central Europe.

For a key to the *Phragmidium* species on *Rosa* see under *Phragmidium mucronatum* (p. 294). For keys to the rusts on *Rubus* see under *Ph. violaceum* (p. 305).

1 *Phragmidium acuminatum* (Fr.) Cooke [non G. Cunn.]

Fig. 101d

Syn. *Phragmidium rubi-saxatilis* Liro

Auteu-form:

0?,I–III on: *Rubus saxatilis*

Spermatogonia not found. – **Aecia** hypophyllous, occasionally also epiphyllous, scattered or in groups, small (0.3–0.5 mm in diam.) or elongated on the nerves (up to 5 mm long), yellow, surrounded by numerous hyaline, cylindrical paraphyses (50–75 × 5–8 µm). – **Aeciospores** 15–29 × 14–26 µm, globoid to ellipsoid; wall 2–3 µm thick, yellow, (verrucose to) echinulate; spines rather coarse; germ pores 3–7. – **Uredinia** hypophyllous, scattered, small, circular, yellow, similar to aecia, surrounded by hyaline, cylindrical-clavate paraphyses (50–80 µm long, up to 16 µm wide above). – **Urediniospores** 23–29 × 20–23 µm, globoid, subgloboid to ovoid; wall 2–3 µm thick, hyaline, echinulate; distance of spines 1.5–2 µm; germ pores indistinct. – **Telia** hypophyllous, single or in groups, small, circular, at times confluent, black. – **Teliospores** 4–8-, mostly 6–7-celled, (30–)72–88(–117) × (20–)27–30(–34) µm, cylindrical with an often rather long, hyaline, ± awl-shaped papilla at the apex (7–18 µm); wall 3–5 µm thick, brown, densely verrucose; germ pores 2–4 per cell; pedicel hygroscopic, mostly longer than the spore, with hyaline wall. – References: Gäumann (1959: 1203–1204), Petrova and Denchev (2004: 103), Helfer (2005: 344).

Remarks. Petrova and Denchev (2004) found only few paraphyses around the aecia and uredinia. *Phragmidium acuminatum* is similar to *Ph. rubi* (syn. *Ph. bulbosum*) (Helfer 2005). Teliospores of *Ph. rubi* have a lower number of cells, and the aeciospores show irregularly slab-shaped wall ornaments. Aeciospores of *Ph. acuminatum* are more echinulate. – The numbers of cells per teliospore given by Gäumann (1959) and Minkevičius (1937) are not accordant with those given by Petrova and Denchev (2004):

- Gäumann (1959): 6.1–6.5 in *Ph. acuminatum*, 5.3–5.7 in *Ph. rubi* (syn. *Ph. bulbosum*);
- Petrova and Denchev (2004): 5.1–6.5 in *Ph. acuminatum*, 5.2–6.6 in *Ph. rubi*.

Phragmidium acuminatum mainly occurs in N Europe and is generally rare in Central Europe. Nevertheless Petrova and Denchev (2004) report its occurrence in Bulgaria. – For records in Austria see Poelt and Zwetko (1997: 94).

(2) *Phragmidium andersonii* Shear

Auteu-form:

(0?,I–III on: *Dasiphora fruticosa* [syn. *Potentilla f.*])

Spermatogonia not found. – **Aecia** hypophyllous, circular (0.5 mm in diam.), orange, surrounded by some paraphyses. – **Aeciospores** 21–28 × 15–25 µm, ellipsoid; wall 1.5–2.5 µm thick, dark yellow, verrucose. – **Uredinia** hypophyllous, circular (0.3 mm), surrounded by many paraphyses. – **Urediniospores** 18–29 × 14–22 µm, obovoid to ellipsoid; wall 1.5–2.5 µm thick, dark yellow, finely verrucose. – **Telia** epiphyllous and hypophyllous, black. – **Teliospores** 3–5-celled, 44–85 × 25–35 µm, cylindrical with short apical papilla (3–5 µm); wall 3–4 µm thick, dark brown; germ pores 2–3 per cell; pedicels long, hygroscopic, with hyaline wall. – Reference: Helfer (2005: 344).

Remarks. *Phragmidium andersonii* has been found in N Europe (e.g., Gäumann 1959; Helfer 2005), and Gäumann (l.c.) supposed its occurrence in relic sites of *Dasiphora fruticosa* in the SW Alps. It is not mentioned by Poelt and Zwetko (1997). Helfer (2005) suspects that *Ph. andersonii* might occur on cultivated *D. fruticosa.*

3 *Phragmidium candicantium* (Vleugel) Dietel

Fig. 87

Syn. *Phragmidium rubi* (Pers.) G. Winter var. *candicantium* Vleugel

Probably Auteu-form:

II,III on: *Rubus* sp., (*R.* ser. *Discolores*, *R. canescens*, *R. constrictus*, *R. grabowskii* [syn. *R. thyrsanthus*], *R. montanus*)

Spermatogonia and aecia unknown. – **Uredinia** hypophyllous, scattered, small, circular, surrounded by club-shaped paraphyses. – **Urediniospores** 21–26 × 16–21 µm, obovoid to ellipsoid; wall 2–3 µm thick, distantly echinulate (0.38–0.46 spines/µm²); distance of spines 2.5–3 µm; germ pores up to 4. – **Telia** hypophyllous, scattered, at times confluent, small, circular, black. – **Teliospores** 5–8-, mostly 6–7-celled, 70–135 × 30–40 µm, cylindrical, with an often short, awl-shaped, hyaline papilla at the apex (nearly as long as in *Ph. rubi*); wall 4.5–6 µm thick, brown, verrucose; warts hyaline; germ pores up to 4 per cell; pedicels usually longer than the spore, hygroscopic, with hyaline wall. – References: Gäumann (1959: 1199), Majewski (1977: 314), Helfer (2005: 346).

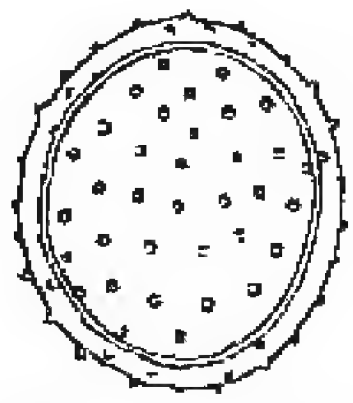


Figure 87. *Phragmidium candicantium* on *Rubus grabowskii* (syn. *R. thyrsanthus*): urediniospore (from Vleugel 1908: 136, with permission from Svenska Botaniska Föreningen).

Remarks. This rust raises questions. Its life cycle and host range are insufficiently known. *Rubus canescens* is listed as host by Helfer (2005). This *Rubus* species is also reported as host of *Phragmidium rubi* (syn. *Ph. bulbosum*), *Ph. violaceum* and *Kuehneola uredinis* (Brandenburger 1994; Petrova and Denchev 2004; Helfer 2005). These rust species also occurs on *Rubus* ser. *Discolores*. *Phragmidium candicantium* can be differentiated by the spacing of echinulation on the wall of the urediniospores and the high number of cells per teliospore (mostly 6–7, sometimes 8). But the number of cells is not a constant character and varies among different collections (Dietel 1927). Wall thickness of urediniospores and spacing of echinulation are more constant characters. – For records of *Ph. candicantium* in Austria see Poelt and Zwetko (1997: 95)

4 *Phragmidium duchesneae* (Arthur) P. Syd. & Syd.

Fig. 88

Syn. *Kuehneola duchesneae* Arthur; *Frommea duchesneae* (Arthur) Arthur; *Frommea obtusa* f. *duchesneae* (Arthur) Arthur; *Frommeëlla duchesneae* (Arthur) Yohem, Cummins & Gilb.; *Frommea mexicana* Mains; *Frommeëlla mexicana* (Mains) McCain & Hennen var. *mexicana*; *Frommeëlla mexicana* (Mains) McCain & Hennen var. *indicae* McCain & Hennen; *Phragmidium mexicanum* (Mains) H.Y. Yun, Minnis & Aime

Brachy-form, probably overwintering in the uredinial stage:

(0,IIa),IIb,III on: *Potentilla indica* [syn. *Duchesnea i.*]

Spermatogonia epiphyllous, in groups on brown necrotic spots, intraepidermal. – **Primary uredinia** surrounding the spermatogonia, orange-yellow when fresh, without paraphyses. – **Primary urediniospores** 15–22 × 13–17 µm; wall 1 µm thick, hyaline, (verrucose-)echinulate. – **Secondary uredinia** hypophyllous, with a few inconspicuous paraphyses, bright orange. – **Secondary urediniospores** 18–24 × 16–18 µm; wall hyaline, about 1 µm thick, finely echinulate; distance of spines 1–1.5 µm; germ pores 3, indistinct. – **Telia** hypophyllous, scattered, small (0.2–0.5 mm in diam.), at times becoming confluent, cinnamon-brown; paraphyses absent. – **Teliospores** not dormant, 50–80 × 19–26 µm, cylindroid to clavoid, 3–5-celled, slightly or not constricted at the septum; wall smooth, cinnamon-brown, 1.5–2 µm thick at sides, 5–10 µm at apex; the wall becomes darker upwards; germ pores 1 per cell, central and apical in the apical cell, immediately below the upper septum in the other cells; pedicels as long as the spore to twice as long, persistent, with hyaline to pale brown wall. – References: McCain and Hennen (1990: 252–254), Poelt and Zwetko (1991: 68), Yun et al. (2011: 1454).

Remarks. Arthur (1912) recognised *Kuehneola duchesneae* as a distinct species for the first time. Sydow and Sydow (1915) transferred this taxon to *Phragmidium*. Arthur (1917) placed it in his new genus *Frommea* (as

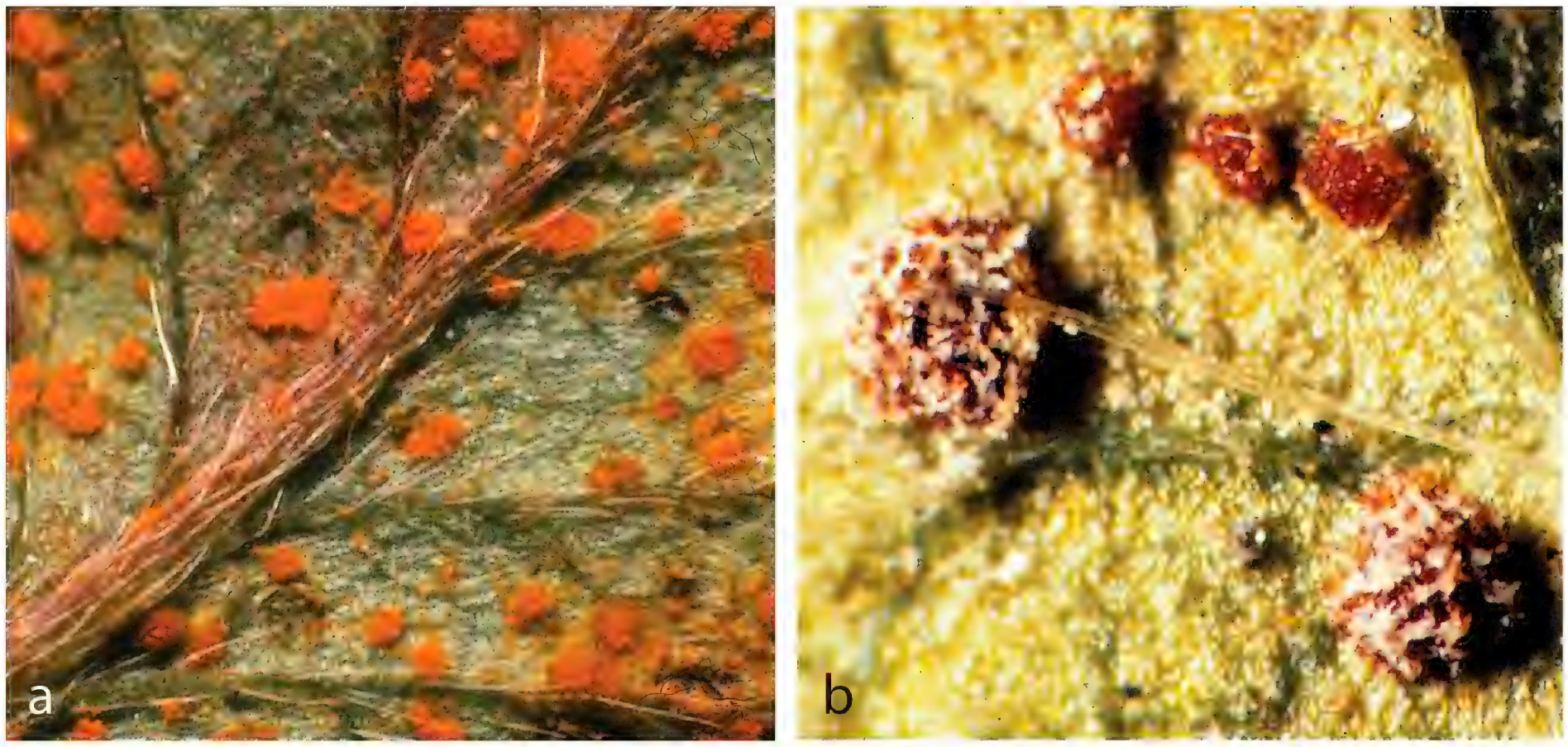


Figure 88. *Phragmidium duchesneae* on *Potentilla indica*: **a.** Orange uredinia; **b.** Telia, the two bigger ones with germinated teliospores bearing a pruina of basidia and basidiospores; (**a** from Poelt and Zwetko 1997: 328).

F. duchesneae) on the basis of having one germ pore per cell in the teliospores and lack of aecia. But his typification of the genus *Frommea* with *Frommea obtusa* (F. Strauss) Arthur (basionym: *Uredo obtusa* F. Strauss) was unfortunate (see the synonyms under *Ph. potentillae* and *Ph. tormentillae*). Therefore, Cummins and Hiratsuka (1983) created the new genus name *Frommeëlla*.

Supposing that Arthur's *Kuehneola duchesneae* is based on a type specimen bearing only the anamorphic, uredinial stage – in spite of Arthur's (1912) description of a telial state, McCain and Hennen (1990) rejected his epithet '*duchesneae*' and created the name *Frommeëlla mexicana* which is based on *Frommea mexicana* Mains (1939). They recognised two varieties, *Frommeëlla mexicana* var. *mexicana* and var. *indicae*, which differ in the number of cells per teliospore and the presence of uredinial paraphyses. The former variety has 2–4 cells per teliospore and no uredinial paraphyses, the latter has 3–5 cells per teliospore and a few uredinial paraphyses. *Frommeëlla mexicana* var. *indicae* corresponds with Arthur's taxon *Kuehneola duchesneae*.

Yun et al. (2011) stated that the combination *Phragmidium mexicanum* is the correct name for this species, because molecular genetic data indicate that *Frommeëlla* is a generic synonym of *Phragmidium*. Examining rust specimens on *Potentilla indica* from the USA and on *P. hebiichigo* from Korea, they found that the presence or absence of uredinial paraphyses was variable in the material studied, and that five-celled teliospores were not consistently encountered in the material from *Potentilla indica*. Additionally, they found no sequence differences that would warrant the recognition of two infraspecific taxa.

In our opinion, doubts on Arthur's type material (E. Bartholomew, Fungi Columbiani 3050) do not justify the nomenclatural changes made later on. Sydow and Sydow (1915) cite this exsiccate and present a complete description of the telial state. On the basis of the knowledge available, we refer to this species as *Phragmidium duchesneae* (Arthur) P. Syd. & Syd.

Poelt and Zwetko (1991, as *Frommeëlla duchesneae*) reported *Phragmidium duchesneae* in Central Europe for the first time. Based on teliospore morphology, Poelt and Zwetko (1997: 61) assigned the Austrian collections to *Frommeëlla mexicana* var. *indicae*. In this area, it is now rather widespread under hedges, in gardens, etc., and probably outlasts winter with urediniospores. Its teliospores germinate without dormancy.

5 *Phragmidium fragariae* (DC.) G. Winter

Fig. 89

Syn. *Puccinia fragariae* DC.; *Puccinia fragariastri* DC.; *Phragmidium fragariastri* (DC.) J. Schröt.; *Phragmidium granulatum* Fuckel

Auteu-form:

0–III on: *Potentilla alba*, *P. argentea*?, *P. caulescens*?, *P. micrantha*, *P. micrantha* subsp. *carniolica*, *P. sterilis*, (*Fragaria vesca*?, *F. viridis*?)

Spermatogonia epiphyllous, subcuticular, sizeable but shallow (15–20 µm high), yellow, sometimes surrounded by the aecia. – **Aecia** mainly hypophyllous, occasionally epiphyllous or on the petioles, round to oblong (0.5–2 mm long), often confluent, sometimes forming circles, orange, surrounded by clavate paraphyses (50–70 × 12–16 µm). – **Aeciospores** 17–28 × 14–24 µm, obovoid, ellipsoid to angular; wall 2 µm thick, hyaline, densely verrucose; warts plateau-shaped, with small spines on the plateau; size of warts variable (up to 3 µm); germ pores indistinct; contents orange. – **Uredinia** hypophyllous, scattered, small, round, surrounded by and including numerous capitate paraphyses (80 × 10–20 µm). – **Urediniospores** 18–25 × 16–22 µm,

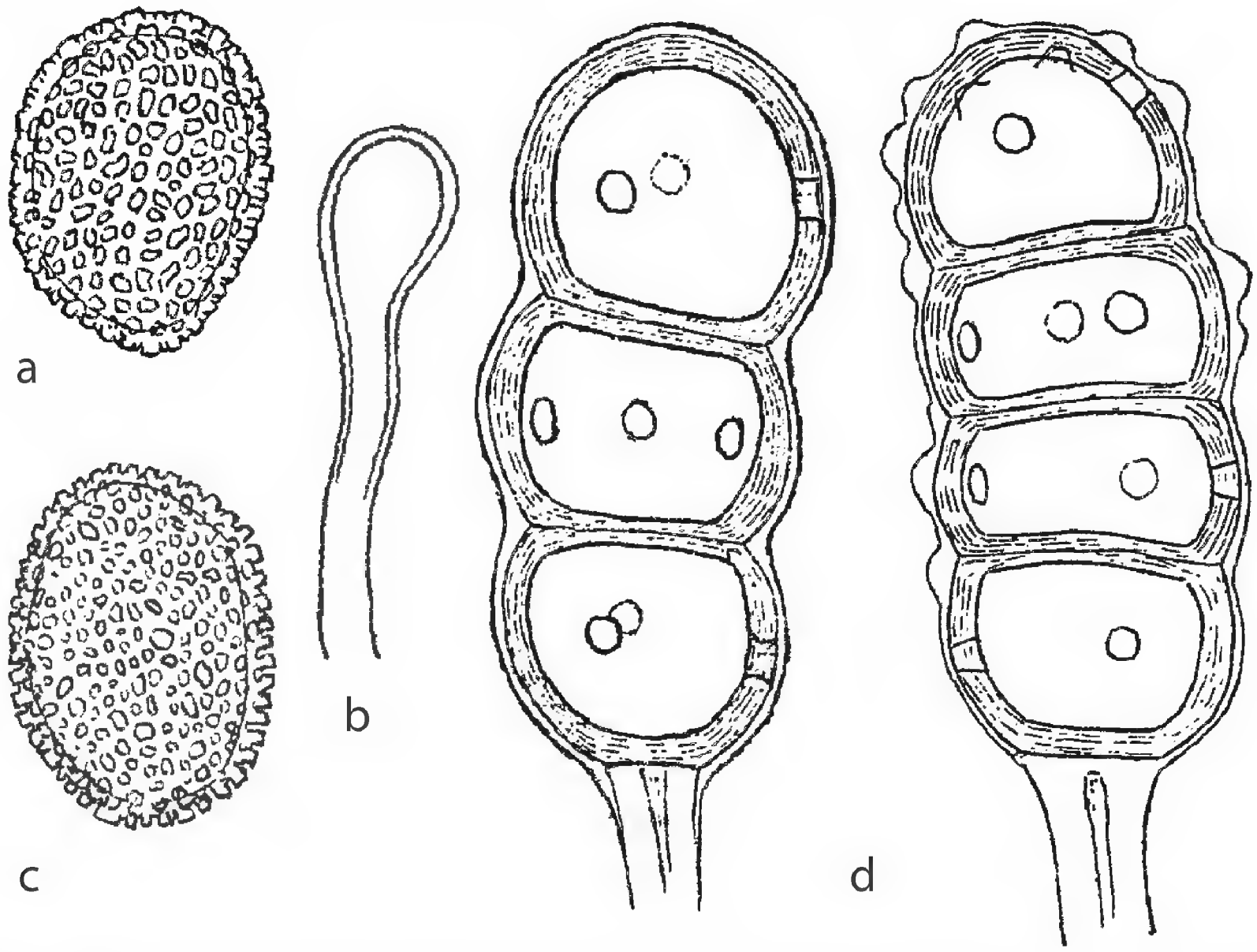


Figure 89. *Phragmidium fragariae*. **a, b.** On *Potentilla sterilis*: **a.** Aeciospore; **b.** Aecial paraphysis; **c, d.** On *Potentilla alba*: **c.** Urediniospore; **d.** Teliospores, the left spore shows that these are sometimes (almost) smooth; (**a–d** from Klebahn 1914: 692, as *Ph. fragariastri*).

globoid to obovoid, orange; wall 2 µm thick, coarsely verrucose; warts plateau-shaped, with small spines on the plateau; size of warts variable (up to 2 µm); germ pores indistinct. – **Telia** hypophyllous, scattered, small, circular, black, soon naked, pulverulent. – **Teliospores** 2–5-, mostly 4-celled, 40–85 × 22–28 µm, rounded at the apex, slightly constricted, never papillate; wall 4 µm thick, pale brown, with some delicate warts around the apex, but often almost smooth; germ pores usually 3, occasionally 2 in each cell; pedicels non-hygroscopic, 15–35 µm, persistent, with hyaline wall. – References: Gäumann (1959: 1179–1180, sub *Ph. granulatum*), Bedlan (1984: 46), Petrova and Denchev (2004: 99), Helfer (2005: 347).

Remarks. In all important European rust florae, *Phragmidium fragariae* is reported to possess aecio- and urediniospores, but its urediniospores are very similar to the aeciospores. According to Bedlan (1984), both kinds of spores have plateau-shaped warts, with small spines on the plateau (like the aeciospores of *Ph. tuberculatum*). This wall ornamentation of urediniospores is a peculiar feature within the Central European *Phragmidium* species. It is very probable that the urediniospores of *Ph. fragariae* are secondary aeciospores.

Braun (1982) listed a record of *Phragmidium fragariae* on *Fragaria viridis* (syn. *F. collina*) from Germany, citing Klebahn (1914), but *F. viridis* is not named as a host in Klebahn's flora. *Fragaria vesca* is treated as an erroneous host record by Petrova and Denchev (2004). Neither *F. vesca* nor *F. viridis* are listed as hosts by Helfer (2005). – For records of *Ph. fragariae* in Austria see Poelt and Zwetko (1997: 95).

There might be more erroneous records of *Phragmidium fragariae* on '*Fragaria*' (strawberries), probably due to the suggestive epithet, perhaps occasionally to the similarity of flowers and leaves of *Potentilla micrantha* and *P. sterilis* to those of *Fragaria* species. However, De Candolle (1807) had the correct host genus in mind when he described his *Puccinia fragariae* on 'potentille fraisier' (*Potentilla fragaria*). But apparently De Candolle did not feel comfortable with the name *Puccinia fragariae* either and re-named the species *P. fragariastri* ('Puccinie du faux-fraisier'), again with 'potentille fraisier' as the host plant (De Candolle 1815). Three entries can be found in World Flora Online (WFO 2024) and Plants of the World Online (POWO 2024) under the name *Potentilla fragaria*: one is unresolved, the second a synonym of *Potentilla sterilis*, the third a synonym of *P. micrantha*. *Potentilla fragariastrum* is a synonym of *P. sterilis*.

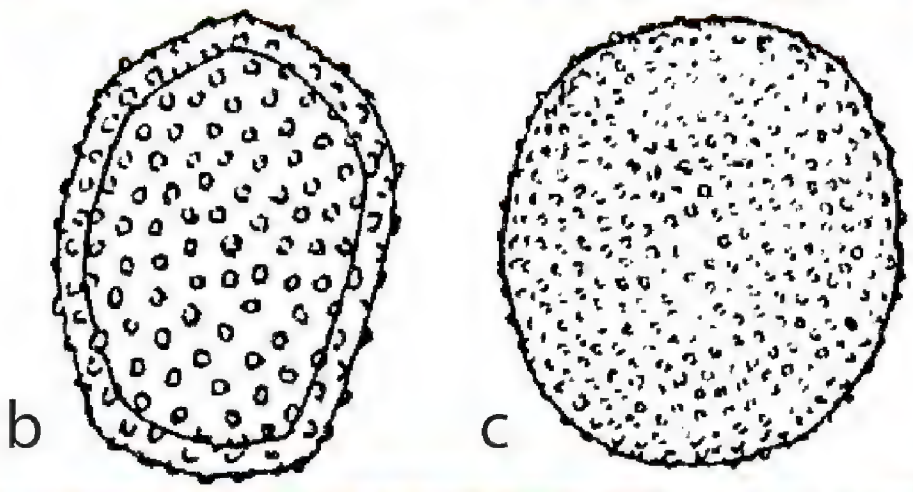
6 *Phragmidium fusiforme* J. Schröt. (var. *fusiforme*)

Figs 90, 92a

Syn. *Phragmidium rosae-alpinae* (DC.) G. Winter

Auteu-form:

0–III on: *Rosa pendulina*, *R. glauca*?, (*R. majalis*, *R. villosa*)



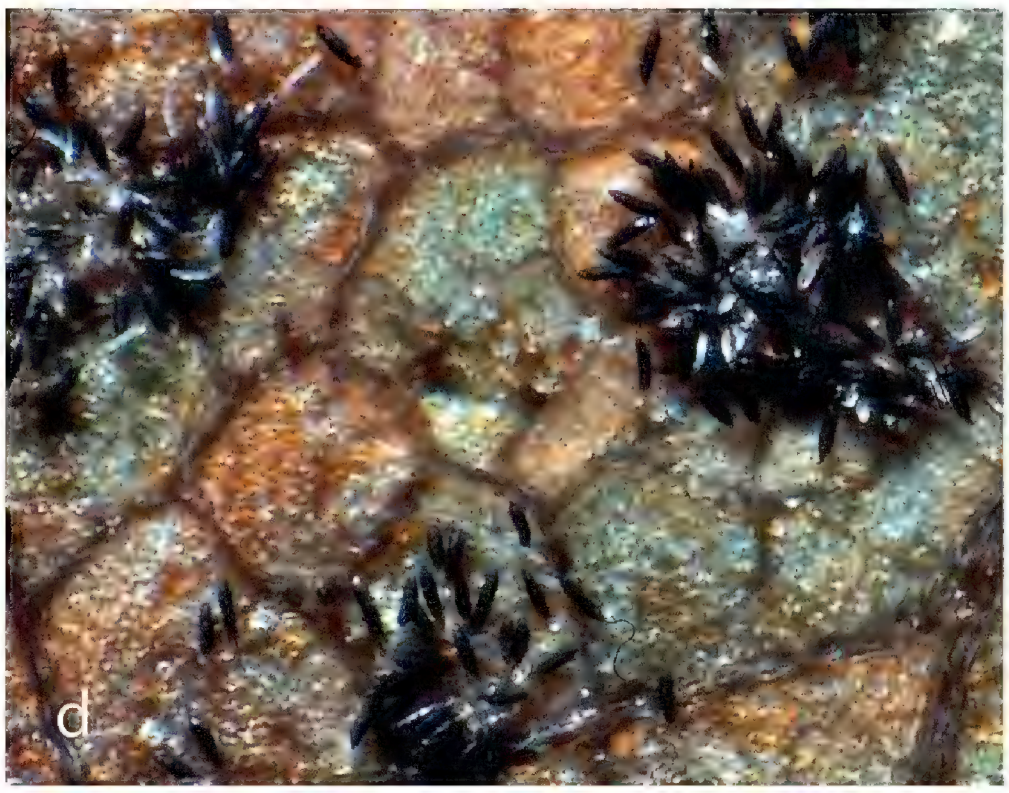


Figure 90. *Phragmidium fusiforme* on *Rosa pendulina*. **a1, a2.** Aecia on stem and leaves; **b.** Aeciospore; **c.** Urediniospore; **d.** Telia with blackish teliospores, many spores already detached by their twisting hyaline pedicels; **e.** Teliospores; (**b, c** from Klebahn 1914: 666; **d** from Poelt and Zwetko 1997: 329).

Spermatogonia epiphyllous, occasionally hypophyllous, subcuticular, 100 µm in diam., 40 µm high. – **Aecia** on leaves, petioles and fruits, large, cushion-shaped on fruits and stems, medium-sized on leaf veins and leaves, round on leaves and fruits, oblong on leaf veins and petioles, orange, surrounded by clavate to capitate paraphyses (70–90 × 10–20 µm). – **Aeciospores** in chains with distinct intercalary cells, 18–30 × 15–21 µm, globoid to angular; wall 1.5–2 µm thick, hyaline, moderately loosely echinulate(-verrucose); spines large, pointed conical; distance of spines about 2 µm (0.58 spines/µm²); germ pores conspicuously capped; number of germ pores 3–5 (after Bedlan 1984), 8–9 (after Henderson and Bennell 1979); contents orange. – **Uredinia** hypophyllous, scattered or in groups, small, punctiform, coalescing at times, surrounded by ± thick-walled paraphyses which are often curving inwards (50 × 8–11 µm). – **Urediniospores** 17–27 × 15–21 µm, globoid to ellipsoid; wall 1.5–2 µm thick, hyaline, echinulate; distance of spines about 1 µm (1.15 spines/µm²); germ pores obscure. – **Telia** hypophyllous, small, punctiform, coalescing at times, black, often originating in the uredinia and therefore surrounded by paraphyses. – **Teliospores** (1–)8–14-celled, mostly 10–12-celled, 42–114 × 21–31 µm, cylindrical to spindle-shaped; apex extended into a horn-shaped or conical papilla; individual cells short; wall 4–5 µm thick, brown, with numerous hyaline warts; germ pores 2–4 per cell; pedicels 60–160 µm long, 15–18 µm wide at the base, hygroscopic, with hyaline wall. – References: Gäumann (1959: 1194–1195), Bedlan (1984: 44), Petrova and Denchev (2004: 107), Helfer (2005: 347–348).

Remarks. *Phragmidium fusiforme* differs from other rusts on *Rosa* by its higher number of teliospore cells (8–14) and by the conspicuous germ pores of aeciospores (see Henderson and Bennell 1979). Its uredinia are smaller than those of *Ph. mucronatum* and *Ph. tuberculatum*, but it is difficult to distinguish *Phragmidium* species on *Rosa* in the uredinial stage. Based on collections of aecia and telia and on inoculation experiments, we can suppose that *Ph. mucronatum* and *Ph. tuberculatum* do not occur on *Rosa pendulina*. Therefore uredinia on this host can be assigned to *Ph. fusiforme*. Gäumann (1959) emphasised that *Ph. fusiforme* has not been examined experimentally.

Phragmidium fusiforme occurs on cultivated *Rosa glauca* (syn. *R. rubrifolia*) in Great Britain, but its occurrence on this host in Austria has not been proved, though the host plant is native in Austria. Nevertheless a *Caeoma* (aecia) found on imported *R. glauca* in Graz might belong to this rust species. Mayor (1969) reported *R. villosa* as host from the French Alps. – For the distribution of *Ph. fusiforme* in Austria see Poelt and Zwetko (1997: 95).

Savile (1974) described *Phragmidium fusiforme* var. *noviboreale* on *Rosa acicularis* from Canada. *Rosa acicularis* is reported as host of *Ph. fusiforme* from Europe (Finland) by Gjærum (1974).

(7) *Phragmidium kamtschatkae* (F.W. Anderson) Arthur & Cummins

Syn. *Puccinia kamtschatkae* F.W. Anderson; *Puccinia rosae* Barclay [nom. illeg.]; *Gymnoconia rosae* Liro; *Phragmidium rosae* (Kuntze) Tranzschel

Micro-form:

(0,III on: *Rosa majalis*)

Spermatogonia amphigenous, more frequently epiphyllous, covering the whole surface of the leaf ± evenly, producing unpleasant smell whilst active. – **Telia** amphigenous, more frequently hypophyllous, roundish, often coalescing, soon naked, pulverulent, dark brown, covering leaves and branches, causing affected leaves to thicken. Perennial mycelium causing loss of shoots and eventually whole plants. – Teliospores 2-celled, at times 1-celled or 3-celled, 30–50 × 16–35 µm, ellipsoid to oblong, slightly constricted; apex round, not thickened; base rounded, rarely tapering slightly; wall yellow-brown, 2–3 µm thick, verrucose; germ pores 1 per cell, occasionally 2 per cell; pedicels 2-celled, the upper cell short, hyaline to yellow, the lower longer and hyaline, ± persistent. – References: Gjærum (1974: 89–90), Helfer (2005: 348).

Remarks. Due to the many two-celled teliospores of this fungus, Gäumann (1959) mentioned this rust in his 'Formenkreis' of *Puccinia tatrensis*. The mycelium is perennial, and it can therefore cause considerable dieback in the affected host (Sydow and Sydow 1904; Helfer 2005). *Phragmidium kamtschatkae* is reported from NE Europe on *Rosa acicularis* and *R. majalis* by Gjærum (1974). It is not mentioned by Poelt and Zwetko (1997).

8 *Phragmidium mucronatum* (Pers.) Schltdl.

Figs 91, 92c

Syn. *Phragmidium disciflorum* (Tode) J. James; *Ph. subcorticium* (Schrank) G. Winter; *Ph. rosae* (Pers.) Rostr.

Auteu-form with repeating aecia:

0–III on: *Rosa ×alba*, *R. arvensis*, *R. canina* [incl. *R. corymbifera*], *R. canina* agg., *R. centifolia*, *R. dumalis* s.l. [syn. *R. coriifolia*], *R. gallica*, *R. spinosissima*? [syn. *R. pimpinellifolia*], *R. tomentosa*, *R. ×turbinata* cult., *Rosa* sp. cult., (*R. agrestis*, *R. centifolia* f. *muscosa* [syn. *R. muscosa*], *R. ×damascena*, *R. elliptica*, *R. foetida*, *R. inodora*, *R. majalis*, *R. marginata* [syn. *R. jundzillii*], *R. micrantha*, *R. mollissima*, *R. moschata*, *R. rubiginosa*, *R. rugosa*, *R. villosa*, *R. virginiana*, *R. dumalis* s.l. [syn. *R. vosagiaca*])

Spermatogonia epiphyllous, occasionally hypophyllous, subcuticular, small and rather flat, 110–115 µm in diam., 35–40 µm high, yellow. – **Aecia** hypophyllous, also on petioles, branches and fruits, roundish, small (1 mm in diam.) but often coalescing on veins, petioles, branches and fruits and then large (up to 10 mm), orange,

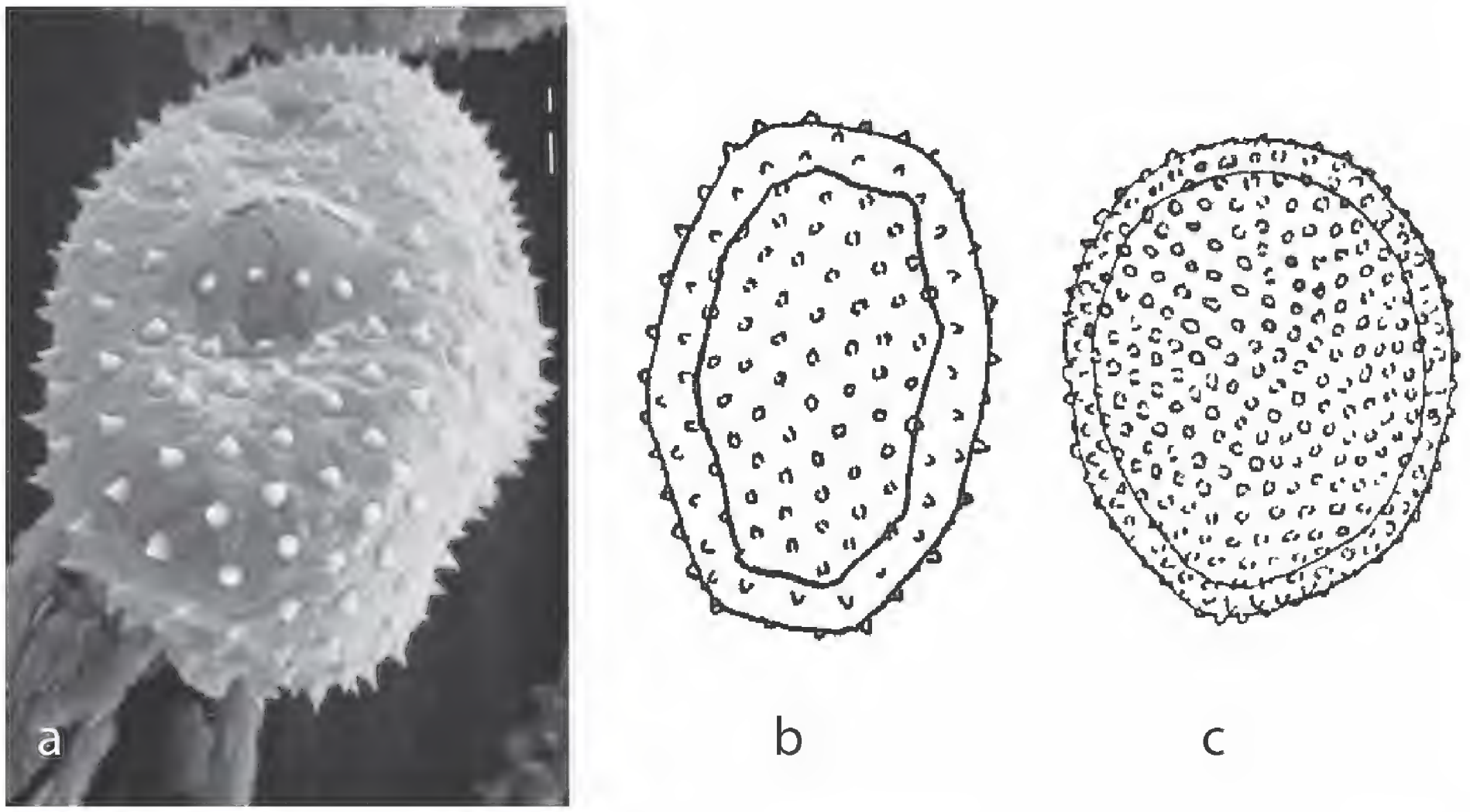


Figure 91. *Phragmidium mucronatum* on *Rosa* spp.: **a.** Aeciospore in SEM; **b, c.** On cultivated roses: **b.** Aeciospore; **c.** Urediniospore; (**a** from Bedlan 1984: 59, with permission from the author; **b, c** from Klebahn 1914: 666, as *Ph. subcorticium*).

often causing yellow or red spots on the upper side of the leaf, surrounded by cylindrical to clavate(-capitate), thin-walled paraphyses, 26–48 µm long after Bedlan (1984), up to 80 µm long after Wilson and Henderson (1966), 8–18 µm wide. – **Aeciospores** 20–30 × 16–21 µm, globoid to ellipsoid; wall (1.5–)2(–3) µm thick, hyaline, distantly echinulate(-verrucose); spines thin and pointed above but with a broad, conical base; distance of spines 2–2.5 µm (0.45–0.58 spines/µm²); germ pores 5–8, scattered, 2–2.5 µm in diam. (smaller and less conspicuous than in *Ph. tuberculatum*). – For transmission electron micrographs of germ pores see Hofsten and Holm (1968) who observed that the spore wall is mostly 1–1.5 µm thick except for some scattered internal, almost globose swellings, where the wall attains at least 2.7 µm. The germ pores appear as areas in the spore wall which are thicker and composed of more electron-transparent material than the rest of the wall. – **Uredinia** hypophyllous, scattered or in groups, small, roundish, 0.1–0.6 mm in diam., soon naked, pale orange, not coalescing, often causing yellow or red spots on the upper side of the leaf, surrounded by paraphyses which are often curving inwards (70 × 7–15 µm). – **Urediniospores** 20–28 × 14–21 µm, globoid to ellipsoid; wall 1.5–2 µm thick, hyaline, closely echinulate (0.77 spines/µm²); germ pores mostly 4–5 after Bedlan (1984), about 8 after Helfer (2005), scattered, small (2–2.5 µm in diam.). – **Telia** originating in the uredinia, hypophyllous, small, punctiform, scattered or in groups, coalescing at times, black. – **Teliospores** 5–9-, mostly 6–8-celled, 65–110 × 22–30 µm, ellipsoid to fusoid, hardly constricted at the septa, rounded at the base; wall 5–7 µm thick, blackish-brown, coarsely verrucose; the upper wall of the uppermost cell gradually tapering into a 7–13 µm long, almost hyaline, distinctly roughened apical papilla; germ pores 2–3 in each cell; pedicels hygroscopic, 130 µm long, swollen at base (22–27 µm), with hyaline wall. – References: Gäumann (1959: 1190–1191), Wilson and Henderson (1966: 104–105), Bedlan (1984: 41–42), Petrova and Denchev (2004: 107–108), Helfer (2005: 349).

Remarks. The host ranges of *Phragmidium mucronatum* and *Ph. tuberculatum* are widely overlapping. The thorn-like spines of aeciospores of *Ph. mucronatum* are very characteristic for this species and differentiate it from *Ph. tuberculatum* (for scanning electron micrographs of aeciospores of *Ph. mucronatum* see also Holm et al. 1970), but it is difficult to distinguish *Phragmidium* species in the uredinial stage. Henderson (2004) emphasised the dimensions of germ pores of aecio- and urediniospores as differential characters: large (4–5 µm in diam.) in *Ph. tuberculatum*; large and conspicuous also in *Ph. fusiforme*; small (2–2.5 µm) in *Ph. mucronatum*. Helfer (2005) measured the spine densities: Urediniospores of *Ph. tuberculatum* have 0.58 spines/µm², those of *Ph. mucronatum* 0.77 spines/µm², and those of *Ph. fusiforme* 1.15 spines/µm². Compared to urediniospores, aeciospores of *Ph. mucronatum* and *Ph. fusiforme* are more distantly echinulate (0.45–0.58 spines/µm² in *Ph. mucronatum*, 0.58 spines/µm² in Ph. fusiforme). However, identification is easier when teliospores are present.

According to Helfer (2005), *Phragmidium mucronatum* is arguably the economically most important rust on ornamental roses. In some years it causes damage in Austria, but *Ph. tuberculatum* occurs more frequently on cultivated roses in our country. – For records of *Ph. mucronatum* in Austria see Poelt and Zwetko (1997: 95–96).

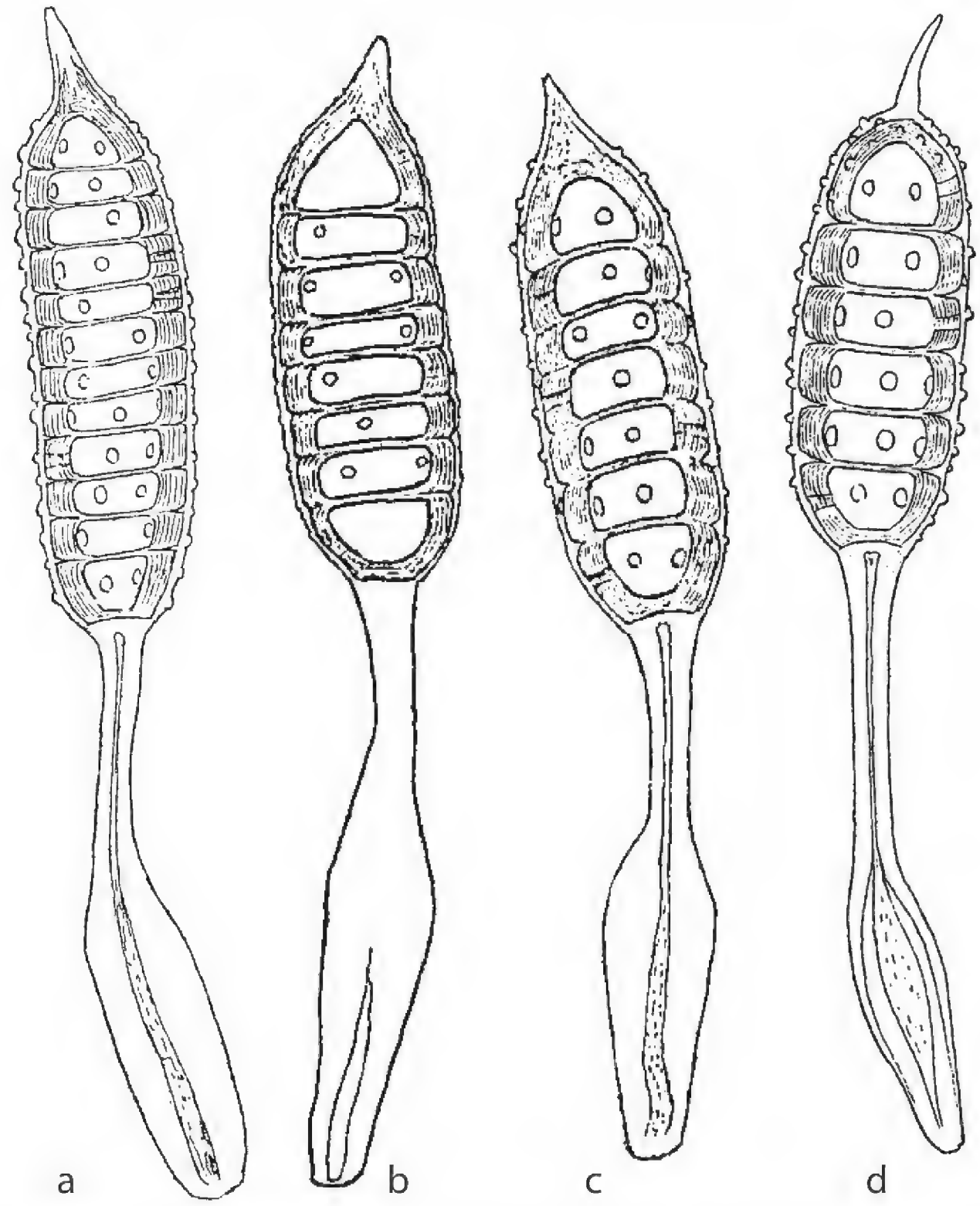


Figure 92. Teliospores of *Phragmidium* species on *Rosa* spp.: **a.** *Ph. fusiforme*; **b.** *Ph. rosae-pimpinellifoliae*; **c.** *Ph. mucronatum*; **d.** *Ph. tuberculatum*; (**a–d** from Klebahn 1914: 666, **c** as *Ph. subcorticium*).

Key to the *Phragmidium* species on *Rosa*

(Fig. 92)

1a Teliospores mostly 2-celled, rarely 3-celled; micro-form without aecia and uredinia ..... *Ph. kamtschatkae*

1b Teliospores more than 3-celled; auteu-forms with aecia and uredinia 2

2a Teliospores reddish-brown, mostly 5–8-celled ..... *Ph. rosae-pimpinellifoliae*

2b Teliospores blackish-brown or black 3

3a Teliospores mostly 5–7-celled, with a rather thin, 15–22 µm long, apical papilla abruptly passing into the apical spore wall; aeciospores coarsely verrucose; aecio- and urediniospores with rather large germ pores (4–5 µm in diam.); spore wall at the germ pore forming hemispherical protrusions far into the lumen of the spore ..... *Ph. tuberculatum*

3b Teliospores mostly 6–8-celled, the spore apex gradually tapering into a 7–13 µm long papilla; aeciospores echinulate, aecio- and urediniospores with smaller pores (2–2.5 µm in diam.); pores less conspicuous ..... *Ph. mucronatum*

3c Teliospores mostly 10–12-celled; aeciospores echinulate, aecio- and urediniospores with large and conspicuous pores; on *Rosa pendulina* ..... *Ph. fusiforme*

9 *Phragmidium potentillae* (Pers.) Corda

Fig. 93

Syn. *Puccinia potentillae* Pers.; *Uredo obtusa* F. Strauss; *Frommea obtusa* (F. Strauss) Arthur [s. F. Strauss, non Arthur, non auct.]

Auteu-form:

0–III on: *Potentilla argentea*, *P. aurea*, *P. crantzii*, *P. caulescens*, *P. heptaphylla*, *P. incana* [syn. *P. arenaria*], *P. inclinata*, *P.* ×*mixta*?, *P. pusilla*, *P. recta*, *P. verna* agg., (*P. anglica*, *P. brauneana*, *P. collina*,

P. erecta, *P. leucopolitana*, *P. micrantha*, *P. neglecta*, *P. norvegica*, *P. prostrata*, *P. patula*, *P. sterilis*?, *P. supina*, *P. verna* s.str. [syn. *P. neumanniana*, *P. tabernaemontani*], *P. wiemanniana* [*P. collina* agg.])

(0–)III on: *Potentilla reptans* – rarely found on this host

Spermatogonia amphigenous, but mostly epiphyllous, at times on petioles, often coalescing, 80–200 µm wide, 25–45 µm high, honey-coloured, often surrounded by the aecia. – **Aecia** mostly hypophyllous, but also epiphyllous and on the petioles, scattered, roundish (0.5–1.5 mm in diam.), often coalescing, orange; surrounded by thin-walled clavate to cylindrical paraphyses (70–80 × 6–10 µm). – **Aeciospores** 18–28 × 14–25 µm, globoid to ellipsoid; wall 1.5–2 µm thick, hyaline, echinulate-verrucose; 'warts' fine, morphologically similar to the spines of the urediniospores (Bedlan 1984); distance of 'warts' about 2 µm (0.58 'warts'/µm²); germ pores indistinct; contents orange. – **Uredinia** hypophyllous, scattered or in groups, small (0.5–1 mm), roundish or elongated, dark orange; at first covered by the swollen epidermis, surrounded by paraphyses which are often curving inwards (50–80 × 10–20 µm). – **Urediniospores** 17–28 × 14–25 µm, globoid to obovoid; wall 1–2 µm thick, pale yellow, finely echinulate; distance of spines 1.5–2 µm

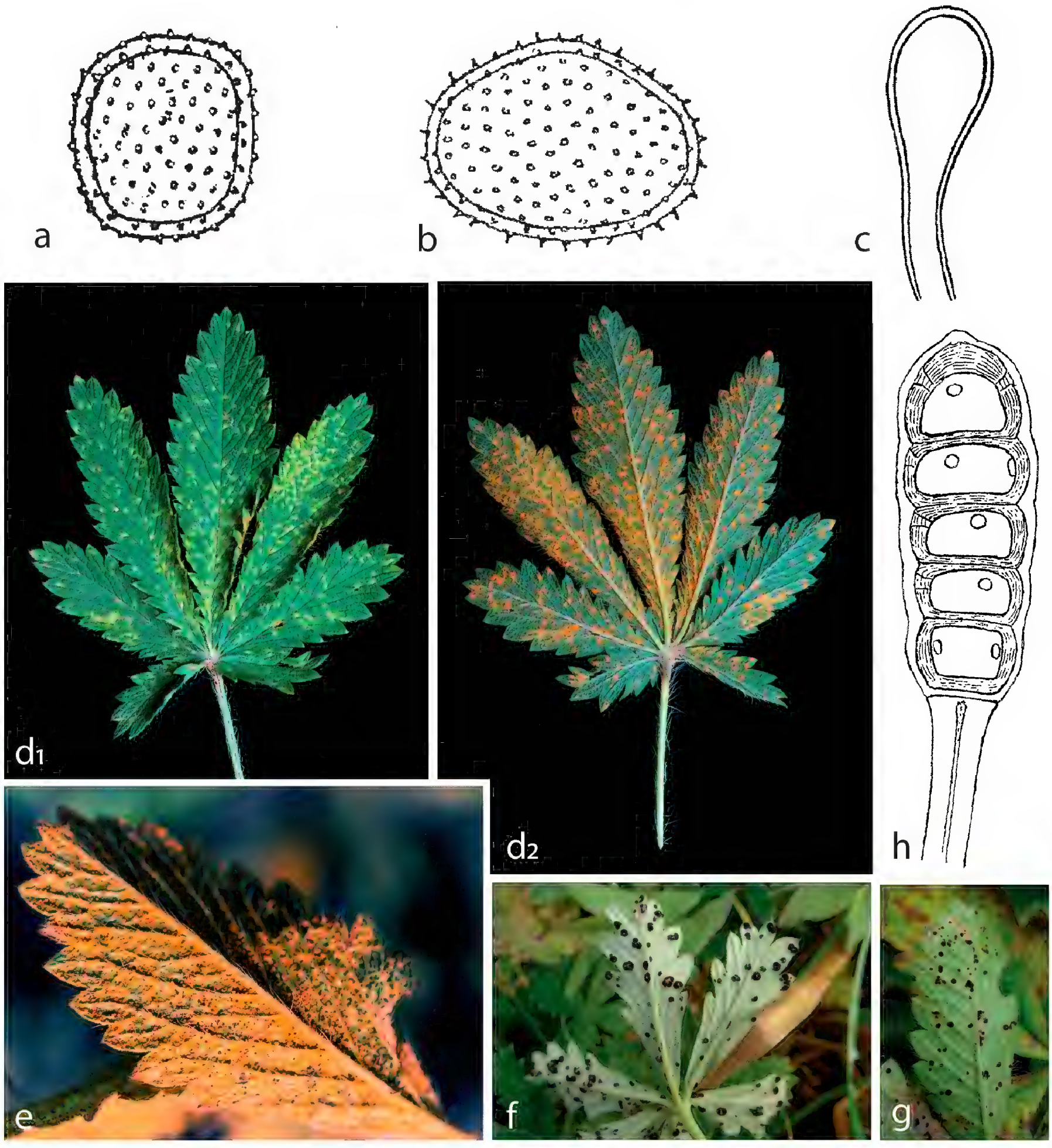


Figure 93. *Phragmidium potentillae*. **a.** On *Potentilla heptaphylla*: aeciospore; **b, c.** On *Potentilla verna* (syn. *P. neumanniana*, *P. tabernaemontani*): **b.** Urediniospore; **c.** Paraphysis; **d, e.** On *Potentilla* trib. *Rectae*: **d1, d2.** Yellow epiphyllous leaf spots and corresponding bright orange uredinia; **e.** Uredinia; **f.** Telia on *Potentilla argentea*; **g.** Telia on *Potentilla norvegica*; **h.** Teliospore; (**a, b, c, h** from Klebahn 1914: 692; **f, g** by Julia Kruse).

(0.46–0.58 spines/µm²); germ pores scattered, indistinct. – **Telia** partly originating in uredinia, hypophyllous, circular, 1 mm in diam., soon naked, cushion-shaped, black, without paraphyses. – **Teliospores** 1–7-, mostly 5–6-celled, 32–108 × 20–30 µm, cylindrical to clavoid, rounded or bluntly papillate at the apex, rounded at the base; wall 3–4 µm thick (up to 10 µm at the apex), dark brown, smooth; germ pores 2–3 in the upper part of each cell; pedicels non-hygroscopic, 60–240 µm long (distinctly longer than the spore), 7–12 µm wide, slightly tapering at the base, persistent, with hyaline wall. – References: Gäumann (1959: 1181–1182), Wilson and Henderson (1966: 101–102), Bedlan (1984: 45–46), Petrova and Denchev (2004: 100), Helfer (2005: 349–350).

Remarks. In contrast to the other *Potentilla* rusts, *Phragmidium potentillae* has a short papilla on its teliospores (Helfer 2005). It can be distinguished from *Ph. fragariae* by the wall ornamentation of its aecio- and urediniospores as well. The host ranges of *Ph. potentillae* and *Ph. fragariae*, and those of *Ph. potentillae* and *Ph. tormentillae* are partly overlapping. In Austria, *Ph. tormentillae* has been found on *Potentilla anglica* (= *P. erecta* × *reptans*) and *P. erecta*. – For records of *Ph. potentillae* in Austria see Poelt and Zwetko (1997: 96).

10 *Phragmidium rosae-pimpinellifoliae* Dietel

Figs 92b, 94

Auteu-form with repeating aecia:

0–III on: *Rosa spinosissima* [syn. *R. pimpinellifolia*], (*R. canina*, *R. foetida*, *R. glauca*, *R. majalis*, *R. rubiginosa*)

(0–III on: *Rosa canina*) – less susceptible host

Spermatogonia mainly on shoots, irregularly scattered, often in groups, 50–120 µm in diam., 15–30 µm high, honey-coloured. – **Aecia** on branches, petioles and veins of leaves and fruits, often confluent to large pustules up to 10 cm long, bright orange, surrounded by cylindric-clavate paraphyses sometimes abundant but usually few or none; paraphyses 30–50 µm long and 10–15 µm wide. – **Aeciospores** 18–27 × 15–20 µm, globoid to ellipsoid; wall 2 µm thick, hyaline, finely echinulate(-verrucose); germ pores 6–8 (after Helfer 2005), 4–5 (after Bedlan 1984), smaller than in *Ph. tuberculatum*; contents orange. – **Uredinia** hypophyllous, scattered, small, circular, 0.1 mm in diam., orange; surrounded by numerous strongly incurved paraphyses (30–50 × 8–12 µm). – **Urediniospores** 18–25 × 16–20 µm, globoid to ellipsoid; wall 2–2.5 µm thick, hyaline, finely echinulate; germ pores 3–4 (after Bedlan 1984), scattered; contents orange. – **Telia** hypophyllous, inside the uredinia or elsewhere, small, circular, 0.1 mm in diam., reddish-brown; sharing the uredinial paraphyses. – **Teliospores** mostly 6–8-celled, 65–115 × 25–34 µm, oblong-cylindric to obovoid-cylindric, not constricted, with conical, pale or hyaline, 14–20 µm long apical papilla; wall 4–6 µm thick, opaque, brown, finely verrucose especially in the upper part, usually nearly or quite smooth below; germ pores (2–)3 per cell; pedicels hygroscopic, firm, about 1.5 times longer than the spore, up to 25 µm wide at the base; wall hyaline except near the spore. – References: Gäumann (1959: 1186–1187), Wilson and Henderson (1966: 103), Bedlan (1984: 43–44), Helfer (2005: 350–351).

Remarks. *Phragmidium rosae-pimpinellifoliae* can cause dramatic dieback as it girdles even thicker branches with its aecia (Helfer 2005). The reddish-brown

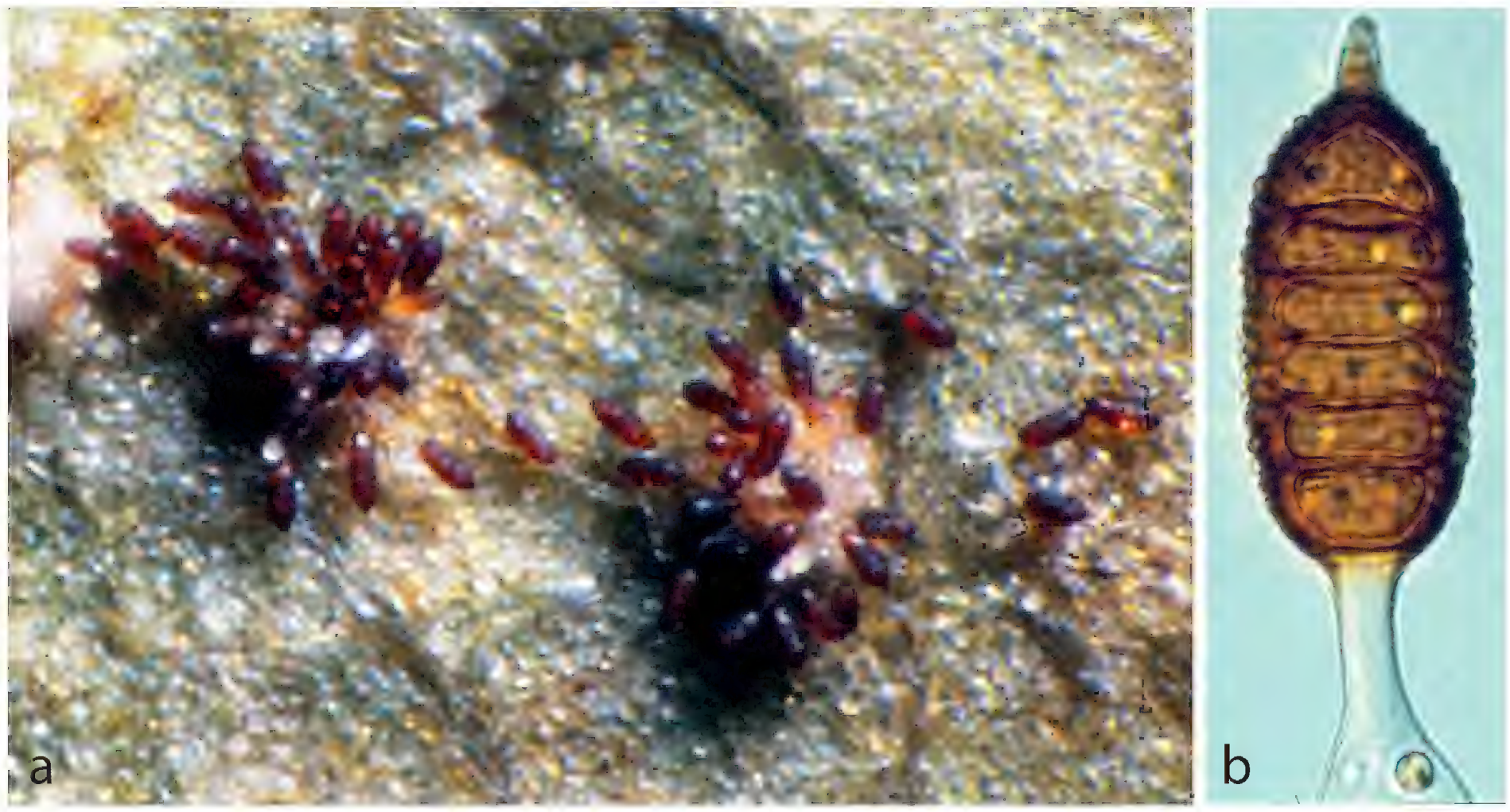


Figure 94. *Phragmidium rosae-pimpinellifoliae* on *Rosa spinosissima*: **a.** Reddish-brown telia; **b.** Teliospore; (**a** from Poelt and Zwetko 1997: 329).

teliospores are very characteristic for this species and differentiate it from *Ph. mucronatum*, which also occurs on *Rosa spinosissima*. It differs from *Ph. mucronatum* also in its slightly smaller aeciospores and aecia surrounded by few or no paraphyses (Wilson and Henderson 1966), but these characters do not permit reliable differentiation in the aecial stage. – For records of *Ph. rosae-pimpinellifoliae* in Austria see Poelt and Zwetko (1997: 96–97).

11 *Phragmidium rubi* (Pers.) G. Winter

Figs 95, 101c

Syn. *Phragmidium bulbosum* (F. Strauss) Link ex J.C. Schmidt & Kunze; *Ph. bulbosum* (F. Strauss) Schltdl.

Auteu-form:

0–III on: *Rubus caesius*, *R.* sect. *Corylifolii*, *R.* ser. *Discolores*, *R. montanus*, *R. nessensis*, *R.* sect. *Rubus*,

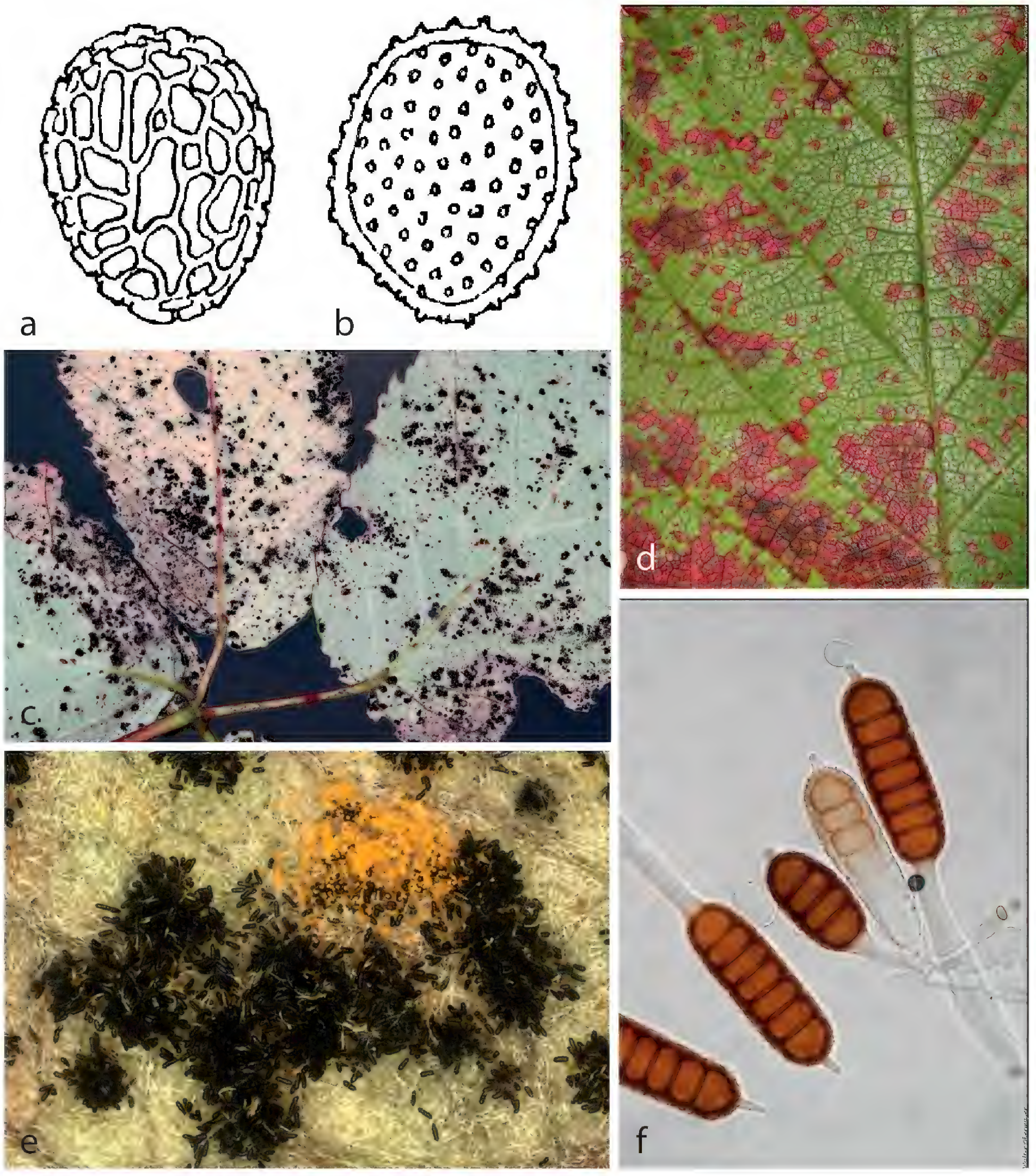


Figure 95. *Phragmidium rubi* (syn. *Ph. bulbosum*) on *Rubus* spp.: **a.** Aeciospore; **b.** Urediniospore; **c.** Telia; **d.** Epiphyllous leaf spots small but confluent; **e.** Blackish telia and one uredinium with orange spores; **f.** Teliospores; (**a, b** from Klebahn 1914: 666; **c–f** by Walter Obermayer).

(*R. bifrons*, *R. canescens*, *R. constrictus*, *R. gracilis*, *R. plicatus*, *R. radula*, *R. rudis*, *R. sprengelii*, *R. sulcatus*, *R. ulmifolius*)

Spermatogonia epiphyllous, subcuticular, in small groups, 75–100 µm in diam, 40 µm high, flat conical, in yellow or reddish spots. – **Aecia** hypophyllous, single or in small groups, 0.5–1 mm in diam. or elongated at the veins, often forming a ring around the spermatogonia, orange, surrounded by hyaline, clavate paraphyses (45–75 × 7–12 µm). – **Aeciospores** in short chains, 20–25 × 15–22 µm, obovoid to ellipsoid; wall 1–2 µm thick, hyaline; surface irregularly slab-shaped, reminiscent of open pack ice, slabs rather large (up to 2–7 × 1–2.5 µm); germ pores 2–4, with hemispherical wall thickenings projecting into the lumen of spore; contents yellow. – **Uredinia** hypophyllous, scattered, yellow, circular (0.3 mm in diam.), confluent at times, surrounded by many clavate, curved paraphyses, often producing yellowish, rarely reddish spots on the upper leaf surface. – **Urediniospores** 20–28 × 14–21 µm, globoid to ellipsoid; wall 1–2 µm thick, yellow, echinulate (0.57–0.8 spines/µm²); distance of spines 1.5–2 µm; germ pores 2–4, with hemispherical wall thickenings projecting into the lumen of spore. – **Telia** hypophyllous, scattered, early exposed, circular (0.5 mm), black. – **Teliospores** 2–7-, mostly 5–6-celled, (30–)60–75(–115) × (18–)25–29(–32) µm, cylindrical, not constricted at the septa, with a hyaline, awl-shaped papilla at the apex (up to 12 µm long after Wilson and Henderson 1966 and Helfer 2005; up to 16 µm long after Petrova and Denchev 2004); wall 5–7 µm thick, brown, coarsely verrucose; warts hyaline; germ pores 2–4 per cell; pedicels hygroscopic, up to 140 µm long, with hyaline wall. – References: Gäumann (1959: 1200–1201), Wilson and Henderson 1966: 95), Petrova and Denchev (2004: 106), Helfer (2005: 345–346).

Remarks. According to Helfer (2005), *Phragmidium rubi* is one of the more common bramble (*Rubus*) rusts, similar to *Ph. violaceum* but with a higher number of teliospore cells and urediniospores with thinner walls. *Phragmidium rubi* and *Ph. violaceum* also differ in surface ornamentation of aecio- and urediniospores. The host ranges of both species are overlapping with that of *Kuehneola uredinis*. – For records of *Ph. rubi* in Austria see Poelt and Zwetko (1997: 94–95, as *Ph. bulbosum*).

12 *Phragmidium rubi-idaei* (DC.) P. Karst.

Figs 96, 101a

Auteu-form:

0–III on: *Rubus idaeus*

Spermatogonia epiphyllous, 45–90 µm in diam., 20–35 µm high, conical, yellow, surrounded by aecia. – **Aecia** epiphyllous, surrounding spermatogonia, in annular groups, at times coalescing and forming small

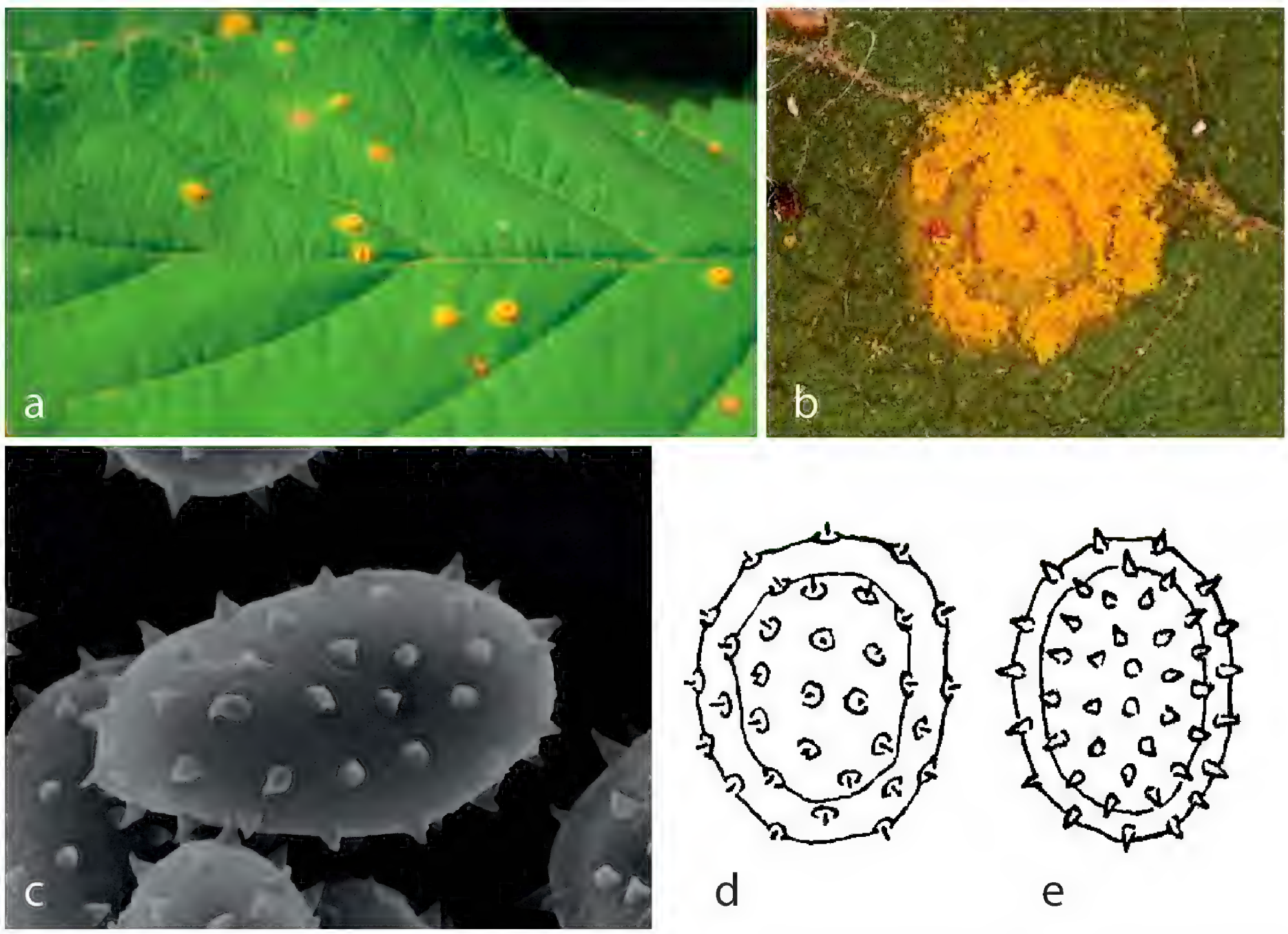


Figure 96. *Phragmidium rubi-idaei* on *Rubus idaeus*: **a, b.** Aecia on the upper side of the leaves, in circular groups; **c, d.** Aeciospores in SEM and a line drawing; **e.** Urediniospore; (**c** by Paul Blanz; **d, e** from Klebahn 1914: 666).

rings (little more than 1 mm in diam.), orange, surrounded by hyaline, clavate, incurved paraphyses (40–70 µm × 14–18 µm) with thin walls. – **Aeciospores** 16–25 × 14–18 µm, obovoid to ellipsoid; wall 2–3 µm thick, pale yellow, distantly echinulate; distance of spines about 4 µm (0.26–0.33 spines/µm²); spines large, with lens-shaped base and fine projection; germ pores obscure. – **Uredinia** hypophyllous, scattered, very small (0.1–0.3 mm in diam.), circular or irregular, pale orange, surrounded by hyaline, thin-walled, clavate, incurved paraphyses (40–70 µm × 14–24 µm). – **Urediniospores** 15–27 × 14–20 µm, broadly ellipsoid; wall 1–3 µm thick, hyaline, sparsely echinulate; distance of spines about 3 µm (0.38 spines/µm²); germ pores obscure; contents orange. – **Telia** hypophyllous, in small groups, very small (0.3–0.7 mm in diam.), circular, black, surrounded by hyaline, clavate, incurved paraphyses (probably when originating in the uredinia). – **Teliospores** 1–14-celled, mostly 7–9-celled, 75–144 × 28–35 µm, cylindrical, rounded at base, rounded or (slightly) tapering at the apex, with ± awl-shaped, hyaline apical papilla (3–15 µm long); wall 3–6 µm thick, dark brown, coarsely verrucose; germ pores 3 per cell; pedicels hygroscopic, longer than spore (up to 165 µm), swelling at base (then 14–27 µm wide); wall of pedicel hyaline except near the spore. – References: Gäumann (1959: 1205–1206), Wilson and Henderson (1966: 96), Petrova and Denchev (2004: 109), Helfer (2005: 351).

Remarks. In Europe, *Phragmidium rubi-idaei* is the only rust on raspberries. It can cause economic losses in plantations (Helfer 2005). In N America, it is also reported from *Rubus occidentalis*, which is cultivated in Austria. – *Phragmidium rubi-idaei* is widespread in Austria, but locally uncommon (Poelt and Zwetko 1997: 97).

13 *Phragmidium sanguisorbae* (DC.) J. Schröt.

Fig. 97

Syn. *Puccinia sanguisorbae* DC.

Auteu-form:

0–III on: *Sanguisorba minor*, *S. minor* subsp. *polygama*, (*S. officinalis*?)

Spermatogonia amphigenous, on purple spots, in rounded groups, subcuticular, rather flat, honey-coloured. – **Aecia** amphigenous, often forming circles around the spermatogonia groups, on leaves 0.2–0.3 mm in diam. (after Petrova and Denchev 2004) or up to 1 mm long, on nerves and petioles larger and elongated (often causing distortions), orange, surrounded by hyaline, clavate, incurved paraphyses (40–80 µm × 7–14 µm). – **Aeciospores** 18–25 × 16–22 µm, globoid to ellipsoid to angular; wall 1–1.5 µm thick, hyaline, densely verrucose (0.77–1.15 warts/µm²); germ pores 6–8, inconspicuous,

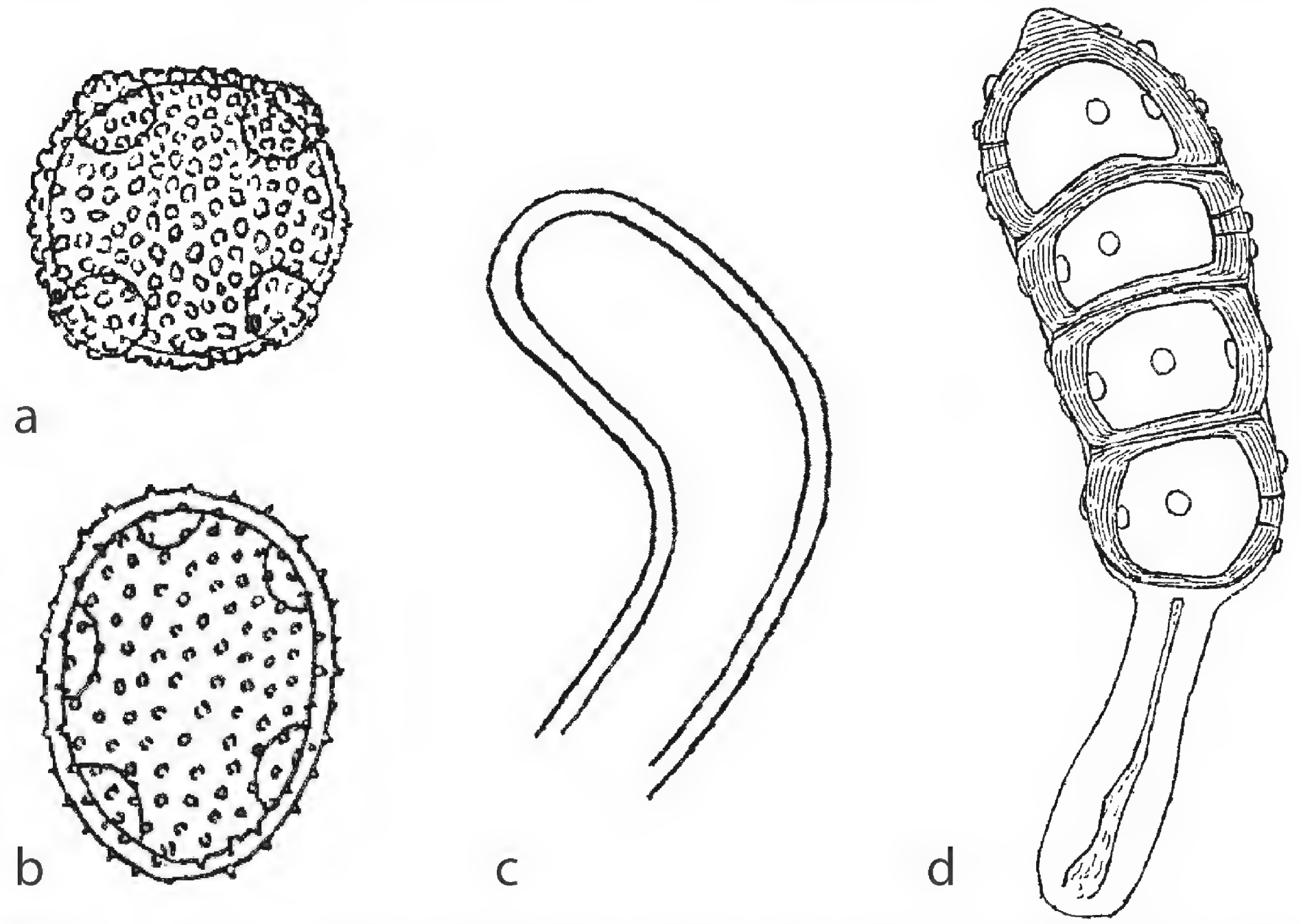


Figure 97. *Phragmidium sanguisorbae* on *Sanguisorba minor*: **a.** Aeciospore; **b.** Urediniospore; **c.** Paraphysis; **d.** Teliospore; (**a–d** from Klebahn 1914: 692).

but spore wall at the germ pore forming hemispherical protrusions into the lumen of the spore; contents orange. – **Uredinia** mostly hypophyllous, occasionally epiphyllous, scattered, small, circular (about 0.25 mm in diam.), soon naked, orange, producing reddish-brown spots on upper leaf surface, surrounded by hyaline, clavate, incurved paraphyses (30–50 µm × 10–17 µm). – **Urediniospores** 17–24 × 15–20 µm, globoid to ellipsoid, orange; wall 1–1.5 µm thick, hyaline, finely echinulate; distance of spines about 1.5 µm (0.77 spines/µm²); germ pores 6–8, indistinct, but pore wall hemispherically thickened and protruding into the lumen of the spore. – **Telia** hypophyllous, small, circular (0.2–0.3 mm in diam.), black, producing spots which are similar to those caused by uredinia, surrounded by hyaline, clavate, incurved paraphyses (40–60 µm long) when originating in uredinia. – **Teliospores** mostly 4-celled, occasionally 2-, 3- or 5-celled, 40–70 × 20–26 µm, ellipsoid-oblong or widely cylindrical, slightly constricted at the septa, rounded at the base, rounded or tapering at the apex, with a short, hyaline, apical papilla (up to 5 µm long), the uppermost cell usually longer than the other cells; wall 3–4 µm thick, brown, with small scattered hyaline warts; germ pores 2–3 per cell; pedicels non-hygroscopic, relatively short (21–28 µm long), persistent. – References: Gäumann (1959: 1183–1185, sub *Ph. poterii*), Bedlan (1984: 47), Petrova and Denchev (2004: 102–103), Helfer (2005: 352).

Remarks. According to Bedlan (1984), the aeciospores of *Phragmidium sanguisorbae* are morphologically similar to those of *Ph. tuberculatum*. Their warts are plateau-shaped, with small spines on the plateaus.

Xenodochus carbonarius also occurs on *Sanguisorba*. Helfer (2005) listed *S. minor* and *S. officinalis* as hosts of both rusts, *Xenodochus carbonarius* and *Phragmidium sanguisorbae*. Contrary to Helfer, Gäumann (1959) reported *S. officinalis* only as host of *X. carbonarius* and *S. minor* only as host of *Ph. sanguisorbae*. The two rusts can be easily distinguished by their teliospores. Records of *Ph. sanguisorbae* on *Sanguisorba officinalis* in Germany proved to be erroneous (Thiel et al. 2023). – For records of *Ph. sanguisorbae* in Austria see Poelt and Zwetko (1997: 97).

14 *Phragmidium tormentillae* Fuckel

Fig. 98

Syn. *Frommea tormentillae* (Fuckel) U. Braun; *Frommeëlla tormentillae* (Fuckel) Cummins & Y. Hirats.; *Xenodochus tormentillae* (Fuckel) Magnus; *Frommea obtusa* auct. [see *Phragmidium potentillae*]

Brachy-form:

0,IIa+b,III on: *Potentilla anglica*, *P. erecta*, (*P.* ×*mixta*, *P. recta*, *P. reptans*)

(II on: *Fragaria viridis*)

Spermatogonia epiphyllous in small groups on reddish and slightly hypertrophic spots, inconspicuous, intraepidermal. – **Primary uredinia** epiphyllous, surrounding the spermatogonia, orange-yellow when fresh. – **Primary urediniospores** 19–28 × 14–18 µm, obovoid; wall 1–1.5 µm thick, hyaline, verrucose-echinulate above, nearly smooth below; germ pores indistinct. – **Secondary**

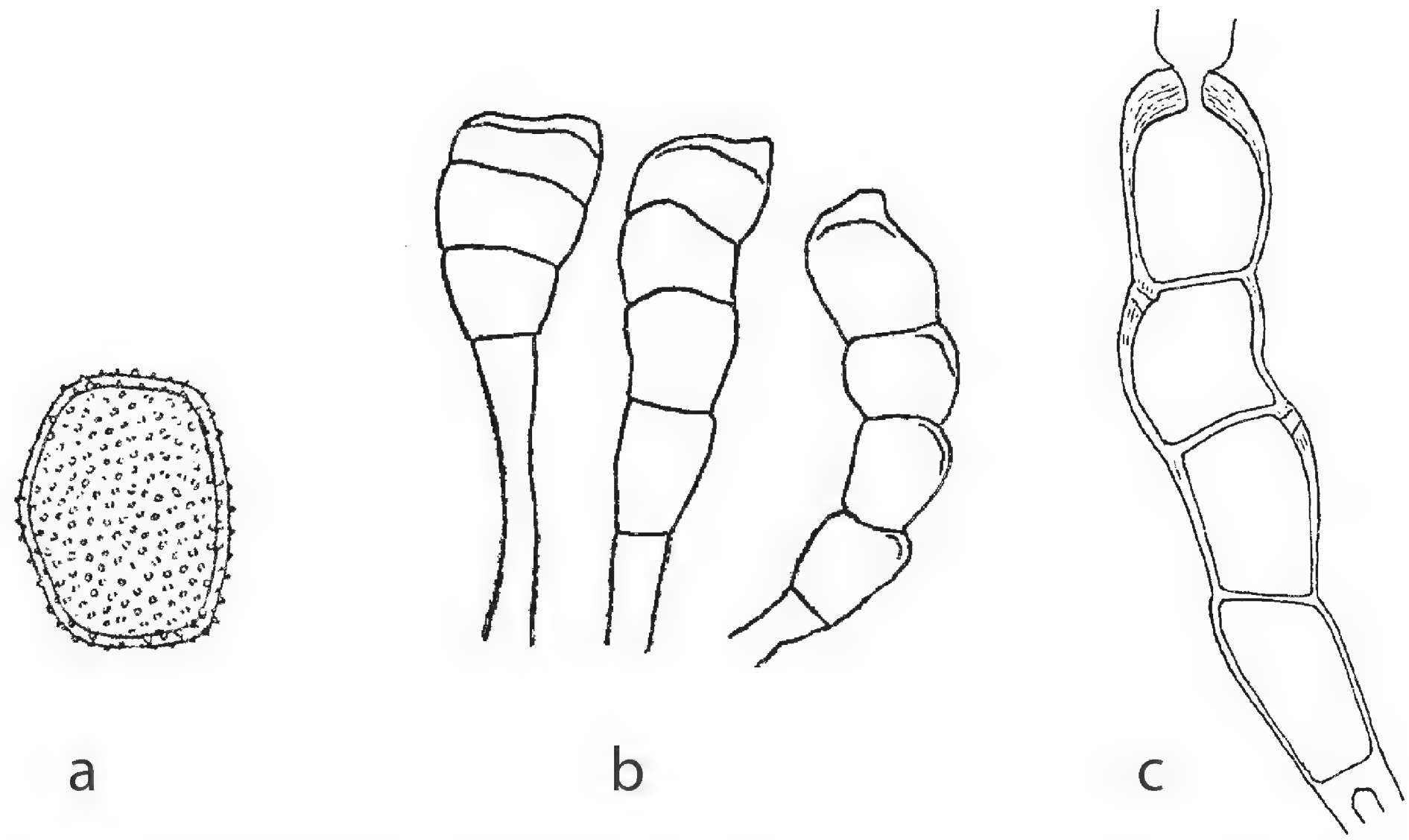


Figure 98. *Phragmidium tormentillae* on *Potentilla anglica*: **a.** Urediniospore; **b.** Teliospores; **c.** Germinating teliospore; (**a–c** from Klebahn 1914: 692, as *Xenodochus t.*).

uredinia hypophyllous, also on petioles, scattered, small, punctiform, light yellow when fresh, with a few peripheral, clavate paraphyses. – **Secondary urediniospores** 16–23 × 13–17 µm, globoid or obovoid; wall hyaline to pale yellow, about 1.5 µm thick, finely echinulate; germ pores 3–4, indistinct. – **Telia** hypophyllous, similar to the secondary uredinia but light cinnamon-brown. – **Teliospores** not dormant, 44–140 × 18–24 µm, 2–7-celled (mostly 5-celled), 44–90 µm long when 3–4-celled, 95–140 µm long when 5–6-celled, cylindroid, fusoid or clavoid, often curved, slightly constricted at septa, tapering below; wall thin at base (1 µm), thickened at the apex (5–8 µm), smooth, hyaline to yellowish-brown; cells becoming darker upwards, the lowermost cell nearly hyaline, the uppermost pale brown; germ pores 1 per cell, central and apical in the uppermost cell, immediately below the upper septum in the other cells; contents orange; pedicels varying in length, persistent, not much widened below; teliospores can germinate in summer and autumn. – References: Gäumann (1959: 1174, as *Frommea obtusa*), Wilson and Henderson (1966: 111, as *Frommea obtusa*), Helfer (2005: 331, 333, as *Frommeëlla tormentillae*), Yun et al. (2011: 1400).

Remarks. *Phragmidium tormentillae* can maintain itself by overwintered urediniospores and mycelium. In our region, it occurs mostly in its uredinial stage which can easily be overlooked or mistaken for *Ph. potentillae*, respectively. According to Gäumann (1959), the discrimination of the two species in their uredinial stage is cumbersome and not easily possible. He referred to statistical spore measurements of Minkevičius (1937). According to these measurements, the mean of the urediniospores of *Ph. tormentillae* on *Potentilla erecta* is 19.2±0.07 µm in length and 16.4±0.05 µm in width. In *Ph. potentillae* on *Potentilla incana* (*P. arenaria*) the corresponding mean is 20.5±0.08 µm in length and 17.8±0.06 µm in width, in *Ph. potentillae* on *Potentilla argentea* the mean is 21.1±0.06 µm in length and 18.5±0.4 µm in width. According to Petrova and Denchev (2004), the mean of the urediniospores of *Ph. potentillae* is 21.0±1.9 µm in length and 17.0±1.5 µm in width.

It is doubtful whether the urediniospores of the two species can be discriminated on the basis of their spore wall ornamentation. Klebahn (1914) believed the echinulation of the spore of *Phragmidium tormentillae* to be slightly finer when compared to that in *Ph. potentillae*. According to Gäumann (1959), in *Ph. tormentillae* the wall of the urediniospores is 1–1.5 µm thick, and the distance of their spines is 1–1.5 µm. In *Ph. potentillae*, the corresponding values are 1.2–2 µm for wall thickness, and 1.5–2 µm for distance between the spines. In Petrova and Denchev (2004) the thickness of the urediniospore wall is 1–1.6(–2) µm in *Ph. potentillae* with a 'finely verrucose' ornamentation.

Also the information on the number and position of germ pores of urediniospores is rather vague: In *Phragmidium tormentillae*, 3–4 germ pores with equatorial position, but hardly detectable (Gäumann 1959); in *Ph. potentillae* germ pores scattered but indistinct (Wilson and Henderson 1966).

At least, the number and shape of paraphyses surrounding the uredinia seem to discriminate between the two species more clearly. According to Wilson and Henderson (1966), numerous peripheric, clavate and curved, up to 80 µm long and 10–20 µm wide paraphyses surround the uredinia of *Ph. potentillae*, while only few clavate paraphyses encircle the uredinia of *Ph. tormentillae*. Majewski (1977) reported on such paraphyses in *Ph. potentillae* reaching even 110 µm in length, while those of *Ph. tormentillae* grow only up to 40 µm.

However, the two species can be discriminated reliably by their telia and aecia/primary uredinia. In *Phragmidium tormentillae*, the aecia are replaced by primary uredinia with single spores on pedicels, while in *Ph. potentillae*, they are developed as caeomata with catenulate spores. In *Ph. tormentillae*, the telia are small (0.5 mm or less in size), light cinnamon-brown with 2–7-celled, mostly 5-celled teliospores, of which each cell shows one germ pore. In *Ph. potentillae*, the telia are larger (1 mm and more in size), black, with 1–7-celled, mostly 5–6-celled teliospores of which each cell shows two or three germ pores. Because of these morphological differences Cummins and Hiratsuka (1983) introduced the nomen novum *Frommeëlla*. This small, autoecious genus is represented by one native and one introduced species in Europe. Its teliospores have only one germ pore per cell and germinate without dormancy, while the teliospores of most *Phragmidium* species have two or three and germinate after overwintering. But analyses of rDNA sequences show that *Frommeëlla* is a generic synonym of *Phragmidium* (Yun et al. 2011).

The host ranges of *Phragmidium tormentillae* and *Ph. potentillae* are widely overlapping. *Potentilla reptans* is reported as host of *Ph. tormentillae* from Great Britain and Ireland (Wilson and Henderson 1966) and from Hautes-Alpes in France (Mayor 1969). – For records of *Ph. tormentillae* in Austria see Poelt and Zwetko (1997: 62, as *Frommeëlla t.*).

15 *Phragmidium tuberculatum* Jul. Müll.

Figs 92d, 99

Auteu-form (without repeating aecia):

0–III on: *Rosa canina* [incl. *R. corymbifera*], *R. canina* agg., *R. majalis*, *R. rugosa*, *R. villosa*, *Rosa* sp. cult., (*R. agrestis*, *R. arvensis*, *R. balsamica* [syn. *R. obtusifolia*], *R. centifolia*, *R. dumalis* s.l. [syn. *R. coriifolia*], *R. gallica*, *R. glauca*, *R. inodora*, *R. mollissima*, *R. multiflora*, *R. rubiginosa*, *R. sherardii*, *R. tomentosa*, *R.* ×*turbinata* cult., *R. virginiana* [syn. *R. lucida*], *R. dumalis* s.l. [syn. *R. vosagiaca*])

Spermatogonia mostly epiphyllous, occasionally hypophyllous, subcuticular, in small groups, conical, 45–122 µm in diam., 20 µm high, honey-coloured. – **Aecia** hypophyllous and on leaf veins, also on branches and pet-

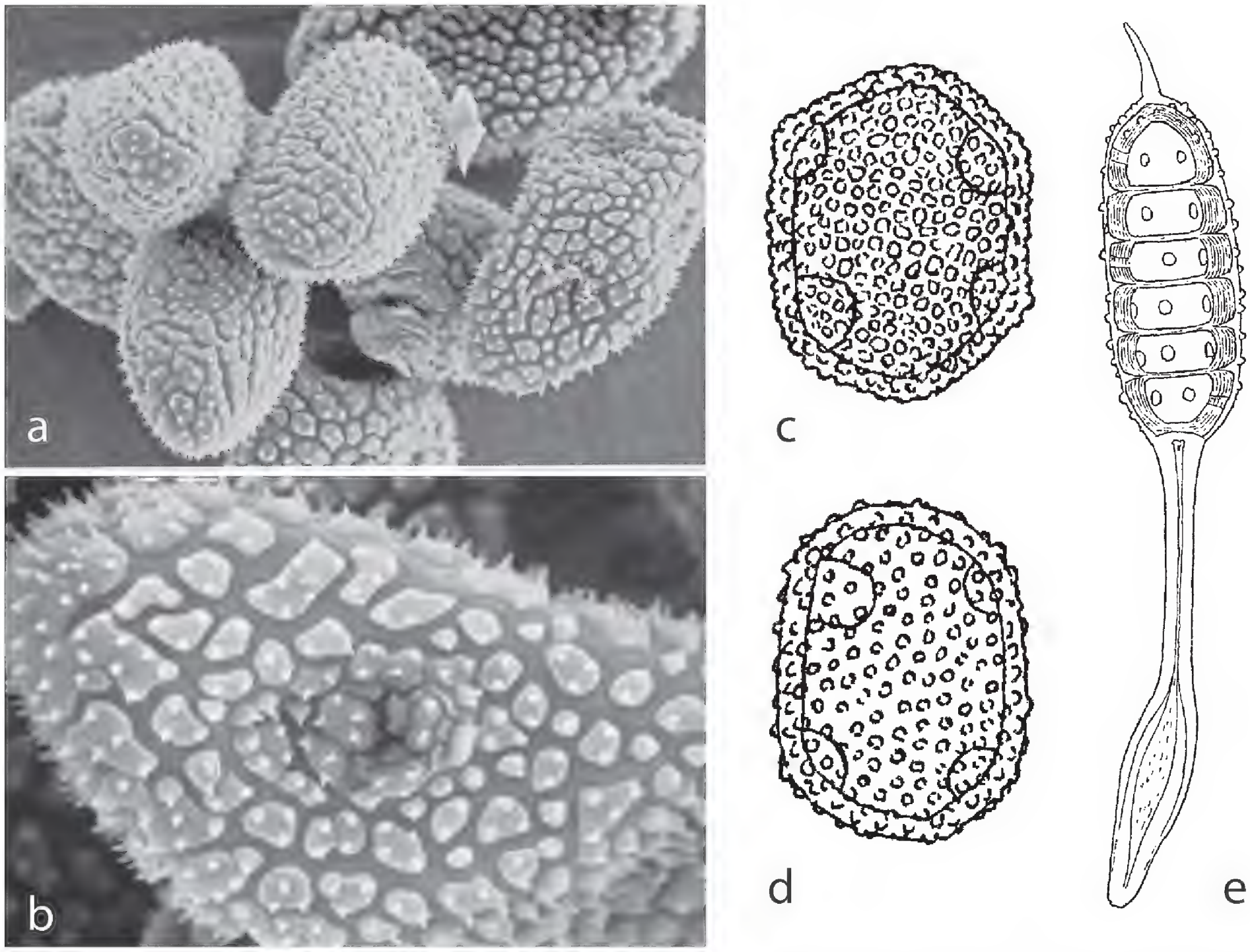


Figure 99. *Phragmidium tuberculatum* on *Rosa* spp.: **a, b.** Aeciospores in SEM; **c.** On *Rosa rubiginosa*, aeciospore; **d.** On *Rosa* sp. cult., urediniospore; **e.** Teliospore; (**a, b** from Bedlan 1984: 58, with permission from the author; **c–e** from Klebahn 1914: 666).

ioles, small and circular on leaves (1 mm in diam.), elongated and larger on branches and petioles (2–3 mm), often coalescing and becoming more than 1 cm large, yellow, producing purple spots on the upper surface, surrounded by hyaline, cylindrical or clavate, ± incurved paraphyses (26–48 × 15 µm after Bedlan 1984). – **Aeciospores** 20–34 × 18–24 µm, globoid to ellipsoid; wall 1.5–2.5 µm thick, hyaline, densely and coarsely verrucose (mean 0.46 warts/µm²); warts plateau-shaped, up to 2 µm wide, with few to several small spines on the plateau; germ pores 6–8, rather large (4–5 µm in diam.), with conspicuous hemispherical protrusions of the pore wall into the lumen of the spore. – **Uredinia** hypophyllous, scattered or in groups, small, circular (0.25 mm in diam.), pale yellow, producing yellow or red spots on the upper surface, surrounded by strongly incurved, clavate paraphyses (30–60 × 6–18 µm). – **Urediniospores** 18–30 × 14–23 µm (after Helfer 2005), 18–23 × 16–18 (after Gäumann 1959), globoid to ellipsoid; wall 1.5 µm thick, hyaline, echinulate-verrucose; spines rather coarse; distance of spines about 1.5 µm (0.58 spines/µm²); germ pores 5–8, with conspicuous hemispherical protrusions of the pore wall into the lumen of the spore (similar to those in aeciospores); contents orange. – **Telia** hypophyllous, scattered or in groups, minute or elongated (up to 1.5 mm), at times coalescing and larger, soon naked, pulverulent, black. – **Teliospores** 2–9-celled, mostly 5–7-celled, (24–)70–90(–138) × (22–)32–36(–42) µm, cylindrical to ellipsoid, hardly constricted at the septa, rounded at base, rounded at apex; the uppermost cell with a pale or hyaline, rather thin, 15–22 µm long, apical papilla abruptly passing into the apical spore wall; wall 5–7 µm thick, dark brown, with small, scattered, hyaline warts; germ pores 2–3 per cell; pedicels hygroscopic, as long as the spore, thickening towards the base (to 14–22 µm), with hyaline wall. – References: Gäumann (1959: 1188), Wilson and Henderson (1966: 106), Bedlan (1984: 39–40), Petrova and Denchev (2004: 109–110), Helfer (2005: 352–353).

Remarks. Analyses of the D1/D2 region of the nuclear 28S rRNA gene (Ritz et al. 2005) indicate that *Phragmidium mucronatum* is closely related to *Ph. fusiforme* and the N American *Ph. montivagum*, all of which parasitise on *Rosa*. Although the host of *Ph. tuberculatum* is *Rosa* as well, it shares a common clade with *Ph. sanguisorbae*, *Ph. rubi-idaei*, *Ph. violaceum* and *Ph. fragariae*. The latter species occur on *Sanguisorba*, *Rubus* and *Potentilla*.

The wall ornamentation of aeciospores of *Phragmidium tuberculatum* is very characteristic and distinguishes it from *Ph. mucronatum* and the two other rusts on *Rosa* occurring in Central Europe, *Ph. rosae-pimpinellifoliae*

and *Ph. fusiforme*. The warts of the aeciospore wall of *Ph. tuberculatum* are plateau-shaped and have an irregularly angular base; the plateaus carry small spines; the distance of spines is 1–2 µm. Bedlan (1984) described this kind of wall ornamentation as 'tuberculatum-type', Wahyuno et al. (2002) as 'echinulate type 3'. The wall ornamentation of aeciospores of *Ph. tuberculatum* is very similar to that of *Ph. sanguisorbae* and *Ph. fragariae* and reflects the phylogenetic relationship of these three species, also indicated by the molecular data mentioned above. The aeciospore morphology of *Ph. mucronatum*, however, resembles that of *Ph. rubi-idaei* and *Ph. violaceum*. Nevertheless, these morphological similarities do not coincide with the molecular data which separate *Ph. mucronatum* from the *Ph. rubi-idaei–Ph. violaceum* clade.

According to Bedlan (1984), the aecia of *Phragmidium tuberculatum* are often coalescing, and become more than 1 cm large. Such large groups of coalescing aecia characterise all rust species on *Rosa* in Central Europe. Therefore, they are no differential characters. However, Helfer (2005) stated that aecia of *Ph. tuberculatum* are smaller in size and are helpful in separating this species from *Ph. rosae-pimpinellifoliae*. Repeating aecia have been observed in inoculation experiments with aeciospores of *Ph. mucronatum* and *Ph. rosae-pimpinellifoliae*, but not with aeciospores of *Ph. tuberculatum* (Bedlan 1984). *Phragmidium tuberculatum* can be distinguished from *Ph. mucronatum* by the large size of its urediniospore germ pores and the abrupt attachment of its teliospore papilla.

According to Poelt and Zwetko (1997: 97), *Phragmidium tuberculatum* is the most common rust on cultivated roses in Austria, but *Ph. mucronatum* occurs more frequently on *Rosa canina* agg.

16 *Phragmidium violaceum* (Schultz) Brockm.

Figs 86, 100, 101b

Auteu-form:

0–III on: *Rubus* sp. [as *R.* '*fuscus*'], *R.* '*fruticosus* agg.', *R.* ser. *Discolores*, *R. apricus*, *R. bifrons*, *R. montanus*, (*R. albiflorus*, *R. canescens*, *R. constrictus*, *R. elatior*, *R. grabowskii* [syn. *R. thyrsanthus*], *R. gracilis*, *R. hirtus*, *R. laciniatus* cult., *R. macrophyllus*, *R. nemoralis*, *R. obtusangulus*, *R. pedemontanus*, *R. phyllostachys*, *R. plicatus*, *R. praecox*, *R. radula*, *R. rudis*, *R. sprengelii*, *R. sulcatus*, *R. ulmifolius*, *R. vestitus*)

(0–III on: *Rubus caesius*) – rarely reported on this host

Spermatogonia epiphyllous, subcuticular, small, hemispherical, densely crowded, usually in the lighter centre of a conspicuous dark violet or reddish leaf spot. – **Aecia** hypophyllous or on stems, scattered or confluent,

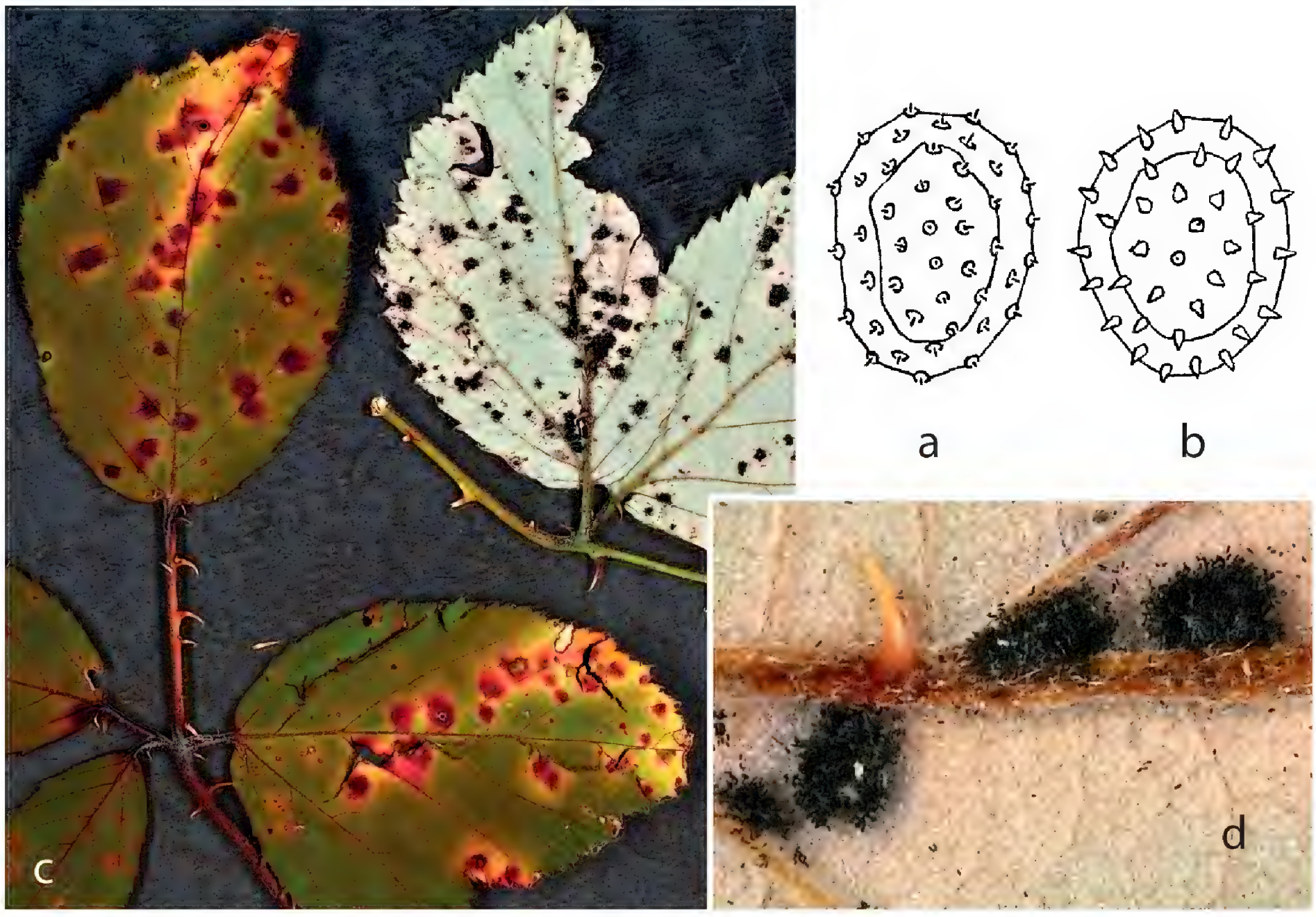


Figure 100. *Phragmidium violaceum* on *Rubus fruticosus* agg.: **a.** Aeciospore; **b.** Urediniospore; **c.** Telia on the lower side of leaves, circular leaf spots with broad purple margin on the upper side; **d.** Close-up of telia; (**a, b** from Klebahn 1914: 666).

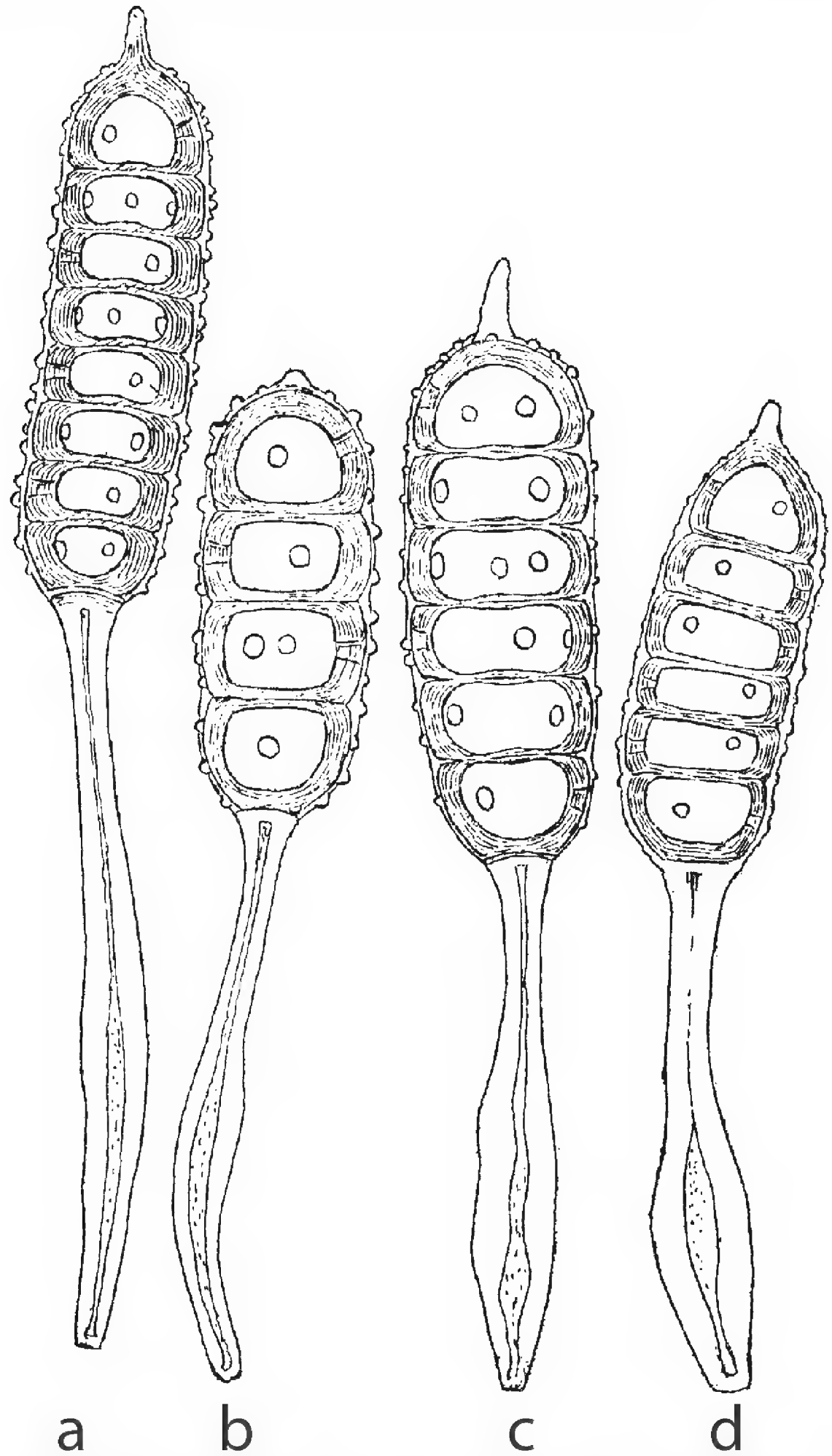


Figure 101. Teliospores of *Phragmidium* species on *Rubus* spp.: **a.** *Ph. rubi-idaei*; **b.** *Ph. violaceum*; **c.** *Ph. rubi* (syn. *Ph. bulbosum*); **d.** *Ph. acuminatum*; (**a–d** from Klebahn 1914: 666, **d** as *Ph. rubi-saxatilis*).

circular to elongated (1 mm in diam., at times up to 10 mm long), orange-yellow, producing conspicuous reddish spots with violet-red margins on the upper surface of the leaf, surrounded by clavate, straight or slightly curved, hyaline paraphyses (up to 60 µm long and 18 µm wide). – **Aeciospores** in short chains with intercalary cells, 19–30 × 17–24 µm, obovoid to ellipsoid; wall 3–4 µm thick, hyaline to yellow, distantly echinulate; spines large, with lens-shaped base and fine projection; distance of spines 4–5 µm (0.23–0.3 spines/µm²); germ pores obscure; contents yellow. – **Uredinia** hypophyllous, on similar spots, small, scattered or confluent, orange-yellow, surrounded by hyaline, clavate or capitate, incurved paraphyses (45–60 × 14–22 µm). – **Urediniospores** 25–32 × 21–24 µm, ellipsoid to ovoid; wall 3–4 µm thick, hyaline, distantly and strongly echinulate; distance of spines 4–5 µm (0.23–0.3 spines/µm²); germ pores obscure; contents yellow. – **Telia** hypophyllous, scattered or confluent, up to 1 mm or more in diam., soon naked, pulverulent, black, producing conspicuous, ± circular reddish spots with broad violet-red margins on the upper surface of the leaf. – **Teliospores** 1–5-celled, mostly 4-celled, 85–110 × 32–35 µm, cylindrical to ellipsoid-oblong, hardly constricted at the septa, rounded at both ends, with a blunt, yellowish papilla at the apex (3–4 µm long); wall 6–9 µm thick, brown, covered by

numerous, hyaline warts; germ pores 3–4 per cell; pedicels hygroscopic, swollen at base, longer than the spore (up to 190 µm long and 18 µm wide), with hyaline wall. – References: Gäumann (1959: 1196–1197), Wilson and Henderson (1966: 98–99), Petrova and Denchev (2004: 110–111), Helfer (2005: 353–354).

Remarks. In many Austrian collections of *Phragmidium violaceum* (and other *Phragmidium* species on brambles), the identification of host taxa needs revision. Often only information like 'on *Rubus* sp.' or 'on *R. fruticosus* agg.' is presented. With W. Maurer's 'Flora der Steiermark' Vol. I (Maurer 1996) and the 'Exkursionsflora für Österreich, Liechtenstein und Südtirol' (Fischer et al. 2008), good keys for identification of *Rubus* species are available. For Germany, Schön (2014) lists 36 *Rubus* species as hosts of *Ph. violaceum*, 15 of *Ph. rubi* (syn. *Ph. bulbosum*), and 23 of *Kuehneola uredinis*. In contrast to *Kuehneola uredinis* which is also found on calyx and stem, *Ph. violaceum* mainly occurs on the leaves. It differs from *Ph. rubi* by its larger, usually circular spots with conspicuous, violet-red margins on the upper surface of the leaves. When plants are very heavily infected, this rust also occurs on peduncles and sepals. – *Phragmidium violaceum* is probably one of the most commonly recorded rusts in Austria (Poelt and Zwetko 1997: 97–98).

Key to the rusts on *Rubus* in the aecial and uredinial stage (on this host genus, aecia and uredinia are often very similar in appearance, even aecio- and urediniospores can readily be confused)

1a Aecia and uredinia without paraphyses 2
1b Aecia and uredinia surrounded by paraphyses ..... (*Phragmidium* spp.) 3
2a Aecia lacking; primary uredinia on the upper surface of the leaf, often confluent into circles; secondary uredinia on the lower surface of the leaf, but also on the stem in deep crevices (up to 1 cm long); mainly on *Rubus* sect. *Rubus* ..... *Kuehneola uredinis*
2b Aecia produced by a systemic mycelium, usually covering the whole lower surface of the leaf; uredinia lacking; on *Rubus saxatilis* ..... *Gymnoconia peckiana*
3a Aecia on the upper surface of the leaf, often confluent into circles; on *Rubus idaeus* ..... *Phragmidium rubi-idaei*
3b Aecia generally on the lower surface of the leaf; on other *Rubus* species than *R. idaeus* 4
4a Wall of aecio- and urediniospores rather thick (3–4 µm), echinulate; distance of spines 4–5 µm ..... *Phragmidium violaceum*
4b Wall of urediniospores thinner 5
5a Wall of urediniospores 2–3 µm thick, echinulate; distance of spines 2.5–3 µm; aeciospores unknown ..... *Phragmidium candicantium*
5b Wall of urediniospores 2–3 µm thick, echinulate; distance of spines 1.5–2 µm; aeciospores verrucose to echinulate ..... *Phragmidium acuminatum*
5c Wall of urediniospores 1–2 µm thick, echinulate; distance of spines 1.5–2 µm; aeciospore surface irregularly slab-shaped (with rather large slabs) ..... *Phragmidium rubi* (syn. *Ph. bulbosum*)

Key to the rusts on *Rubus* in the telial stage

(Fig. 101)

1a Teliospores yellowish to whitish, arranged in chains (mostly composed of 5–7 spores); each spore with ± thickened upper transverse wall; each chain with a short and thin-walled basal cell (pedicel); mainly on *Rubus* sect. *Rubus* ..... *Kuehneola uredinis*
1b Teliospores dark brown, borne singly on thin pedicels; spores mostly 2-celled; transverse walls not thickened; on *Rubus saxatilis* ..... *Gymnoconia peckiana*
1c Teliospores black, borne singly on swelling hygroscopic pedicels (as long as the spore or longer); spores (2–)3–many-celled; transverse walls not thickened; on various *Rubus* species ..... (*Phragmidium* spp.) 2
2a On *Rubus idaeus* and *R. saxatilis* 3
2b On other *Rubus* species 4
3a Teliospores mostly 6–7-celled, with an often rather long, ± awl-shaped papilla at the apex (up to 18 µm); on *Rubus saxatilis* ..... *Phragmidium acuminatum*
3b Teliospores mostly 7–9-celled, with a ± awl-shaped papilla at the apex (3–13 µm long); on *Rubus idaeus* ..... *Phragmidium rubi-idaei*
4a Teliospores mostly 4-celled, with a blunt papilla at the apex (3–4 µm long) ..... *Phragmidium violaceum*
4b Teliospores mostly 5–6-celled, with an awl-shaped papilla at the apex (up to 12 µm long) ..... *Phragmidium rubi* (syn. *Ph. bulbosum*)
4c Teliospores mostly 6–7-celled, with an often short, awl-shaped papilla at the apex .... *Phragmidium candicantium*

Trachyspora Fuckel

A small genus of four species on *Alchemilla* (Rosaceae). – **Spermatogonia** not found in Europe till now. Gjærum and Cummins (1982) reported spermatogonia from E Africa. – **Aecia** subepidermal, erumpent, without peridium or paraphyses, bright orange to yellowish. – **Aeciospores** bright orange when fresh; wall hyaline or pale yellowish, thin, densely echinulate; germ pores obscure. – **Telia** subepidermal, erumpent, without paraphyses, at first produced on systemic mycelium in the old aecia, later on localised mycelium. – **Teliospores** borne singly on pedicels, 1-celled; wall thick, pigmented or nearly hyaline, coarsely verrucose, verruculose or smooth; germ pores obscure; pedicel deciduous.

The aeciospores of the genus *Trachyspora* have been defined by several authors as urediniospores or 'uredinioid aecidiospores' (e.g., Gäumann 1959; Wilson and Henderson 1966; Gjærum 1974; Helfer 2005; Klenke and Scholler 2015). Henderson (1973) studied the ultrastructure and development of these spores, and the ontogeny of the spine-like surface sculpture confirmed that these spores are aeciospores.

Key to the *Trachyspora* species in Europe

1a With aecia and telia (on the *Alchemilla vulgaris* group) ..... *T. alchemillae* (syn. *T. intrusa*)
1b With few aeciospores in the telia; aecia lacking 2
2a Mean dimensions of teliospores: 29.3–30.9 × 27.1–27.7 µm (on *A. hoppeana* and related alpine species) ..... *T. melospora*
2b Mean dimensions of teliospores: 35.0 × 27.6–28.6 µm (on *A. pentaphyllea*) ..... *T. pentaphylleae*

1 *Trachyspora alchemillae* (Pers.) Fuckel

Fig. 102

Syn. *Uromyces alchemillae* (Pers.) Lév.; *Trachyspora intrusa* (Grev.) Arthur

Autopsis-form:

I,IIIa+b on: *Alchemilla* ser. *Pubescentes*, *A.* ser. *Vulgares*, (*A.* ser. *Splendentes*)

Spermatogonia lacking. – **Aecia** arising from a systemic mycelium, hypophyllous, ± covering the lower leaf surface, pulverulent, bright orange when fresh. Infected leaves are usually paler and smaller with longer petioles; infected rosettes do not flower. – **Aeciospores** 16–25 × 14–21 µm (after Helfer 2005: 358), 20–25.5 × 18–22.5 µm, mean 22.6±1.3 × 20.2±1.0 µm (after Petrova and Denchev 2004: 112), bright orange when fresh; wall hyaline, thin, densely echinulate; germ pores obscure. – **Primary telia** soon replacing the aecia, with the same distribution, hypophyllous, pulverulent, light to dark (red-)brown. – **Secondary telia** arising from a limited mycelium later in the season, circular, small and scattered. – **Teliospores** 20–40 × 20–30 µm (after Helfer 2005), 28–37 × 24.5–31 µm, mean 32.3±2.2 × 27.8±1.6 µm (after Petrova and Denchev 2004); wall light brown, irregularly and coarsely verrucose on top, lower part smooth to verrucose, warts sometimes coalescing and forming coarse ridges. – References: Helfer (2005: 358), Petrova and Denchev (2004: 110).

Remarks. More precise or reliable determinations of the host plants recorded in Austria would be desirable, but also

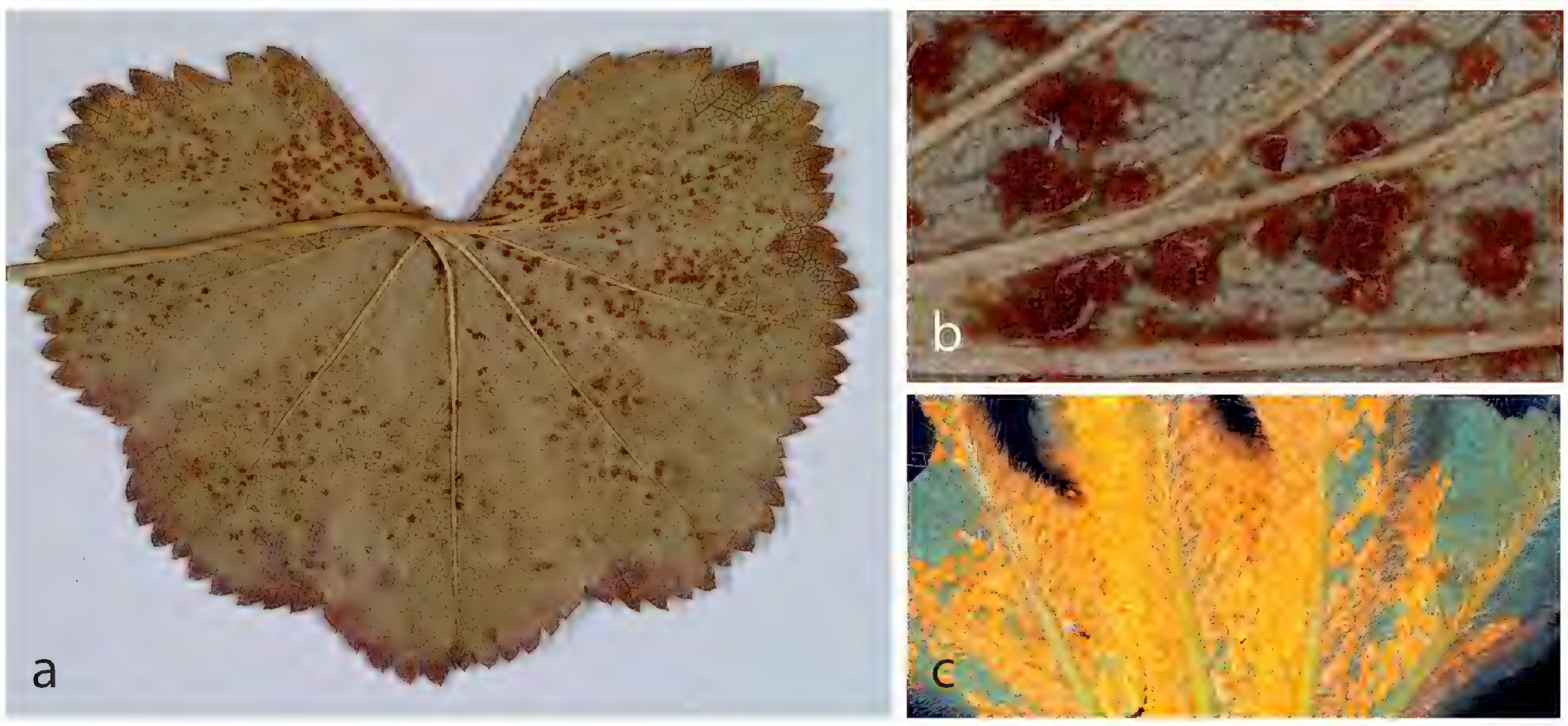


Figure 102. *Trachyspora alchemillae*. **a, b.** Telia on *Alchemilla glabra* (ser. *Vulgares*); **c.** Aecia on *Alchemilla* sp. (ser. *Vulgares*); (**c** from Poelt and Zwetko 1997: 332, as *T. intrusa*).

the taxonomy of this rust should be revised. So far, the host specificity of *Trachyspora* species has not been examined sufficiently either. At any rate, Fischer (1916, cited in Gäumann 1959) has shown by experiment that *Trachyspora alchemillae* can be transmitted by aeciospores from *Alchemilla* sect. *Vulgares* to sect. *Splendentes* and *Pubescentes*, but not to *A. alpina* s. latiss. (sect. *Alpinae* and *Glaciales*) or *A. pentaphyllea* (sect. *Pentaphylleae*), a clear indication that our three taxa are not conspecific. The life cycle of *T. alchemillae* in the northernmost part of Scandinavia resembles the life cycles of *T. melospora* and *T. pentaphyllae* in the Alps. Wilson and Henderson (1966) summarised the results of Scandinavian investigators. They have shown that to the North and at greater altitudes there is an increase in teliospore production together with a decrease in the number of aecia until ultimately the latter disappear completely, usually only a few aeciospores occurring in the telia. Under extreme climatic conditions when the rust produces only telia, the infected leaves exhibit no or only slight abnormalities and the rosettes upon which they are borne often flower.

Trachyspora alchemillae is quite common in Austria, predominantly at montane to subalpine altitudes (Poelt and Zwetko 1997: 255).

2 *Trachyspora melospora* (Therry) Dietel

Fig. 103

Syn. *Uromyces melosporus* (Therry) Syd. & P. Syd.; *Uromyces alchemillae-alpinae* E. Fisch.

Micro-form, tending towards lepto-form:

[I],III on: *Alchemilla alpina* s. latiss., *A.* '*plicatula*' [*A. alpigena* or *A. nitida*] (*A. alpina*?, *A. hoppeana*)

Spermatogonia lacking. – **Aecia** unknown, but a few aeciospores occur among the teliospores in the telia. – **Aeciospores** 21–28 × 18–21 µm, bright orange when fresh; wall hyaline, thin, densely echinulate; germ pores obscure. – **Telia** arising from a systemic mycelium, ± covering the leaf surface, hypophyllous, pulverulent, brown. Infected leaves are usually paler and smaller with longer petioles; infected rosettes flower sometimes. Secondary telia unknown. – **Teliospores** (23–)27–32(–45) × (19–)26–30(–37) µm, mean 29.3–30.9 × 27.1–27.7 µm (after Gäumann 1959); wall light brown, irregularly and coarsely verrucose, rarely smoother. – Reference: Gäumann (1959: 217).

Remarks. Apparently *Trachyspora melospora* grows on species of *Alchemilla* sect. *Alpinae* and sect. *Glaciales* (as delimited in Fischer et al. 2008), mainly from the altomontane to the alpine belt. It has only been found in a few scattered localities in W Austria (Poelt and Zwetko 1997: 255).

(3) *Trachyspora pentaphylleae* Gäum.

Syn. *Trachyspora melospora* (Therry) Dietel var. *pentaphylleae* (Gäum.) S. Helfer

Micro-form:

([I],III on: *Alchemilla pentaphyllea*)

Spermatogonia lacking. – **Aecia** unknown but a few aeciospores occur among the teliospores in the telia. – **Aeciospores** 20–26 × 18–21 µm; wall thin, pale yellowish, densely echinulate. – **Telia** as in *T. melospora*. – **Teliospores** (26–)32–39(–48) × (19–)26–30(–37) µm, mean 35.0 × 27.6–28.6 µm (following Gäumann 1959); wall light brown, irregularly and coarsely verrucose, rarely smoother. – Reference: Gäumann (1959: 218).

Remarks. The species was hitherto known only from Switzerland. Petrova and Denchev (2004) also assigned rust collections on *Alchemilla connivens*, *A. erythropoda* and *A. viridiflora* from Bulgaria to *Trachyspora pentaphylleae*. Teliospore dimensions of Bulgarian specimens: 32.5–43 × 24.5–33 µm, mean 36.0±2.9 × 29.1±2.1 µm.

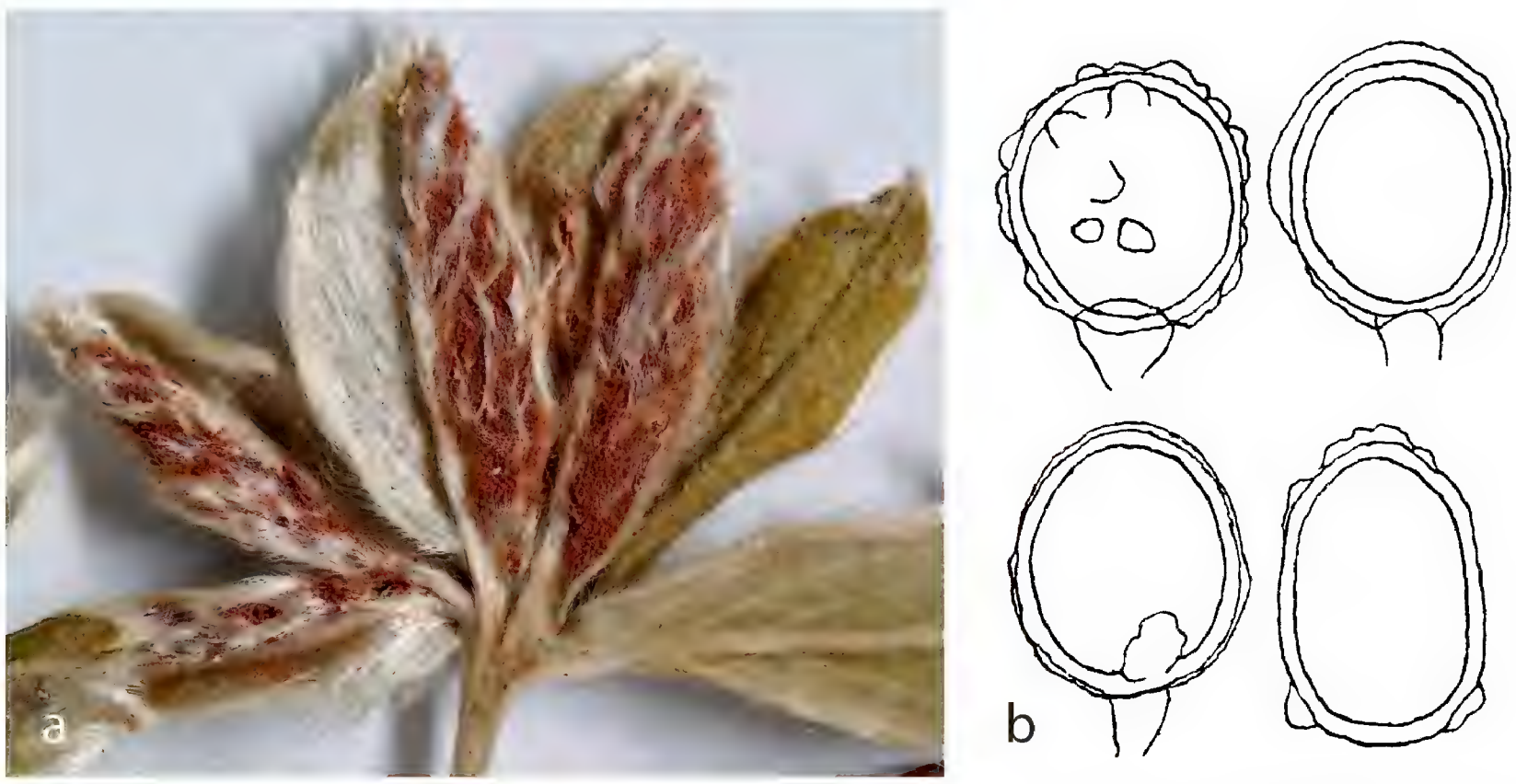


Figure 103. *Trachyspora melospora*. **a.** Telia on *Alchemilla* '*plicatula*'; **b.** Teliospores; (**b** from Fischer 1904: 47, as *Uromyces Alchimillae alpinae*, with permission from Bryolich).

Triphragmium Link

The genus has been revised and classified into two species by Lohsomboon et al. (1990b); both occur on *Filipendula* (Rosaceae) and are represented in Europe. The genera *Triphragmiopsis*, *Triphragmium* and *Nyssopsora* are characterised by 3-celled teliospores. *Triphragmium* differs from *Triphragmiopsis* and *Nyssopsora* in the number of germ pores in each teliospore cell; *Triphragmium* has only one, whereas the two other genera have two or more. Both *Triphragmium* species cause conspicuous distortions in their host plants.

1 *Triphragmium filipendulae* (Lasch) Pass.

Fig. 105c, d

Brachy-form:

0,IIa+b,III on: *Filipendula vulgaris*

Spermatogonia hypophyllous or petiolicolous, subcuticular, flat, yellow. – **Primary uredinia** amphigenous, mostly on the petioles or leaf veins, circular to elongated, up to 20 mm long, subepidermal in origin, then erumpent, pulverulent, orange; causing conspicuous distortions of the leaves. – **Primary urediniospores** borne singly on pedicels, irregular in shape, pyriform to ellipsoid to ovoid, 27–34 × 22–26 µm (mean 30 × 23 µm); wall 1–2 µm thick, hyaline, echinulate but sometimes smooth basally; distance of spines 2–2.5 µm; germ pores obscure; contents orange. – **Secondary uredinia** hypophyllous, scattered, circular, 1 mm in diam., orange. – **Secondary urediniospores** very similar to primary urediniospores but slightly smaller, 21–31(–33) × 21–24(–27) µm (mean 27 × 22 µm). – **Telia** hypophyllous, scattered, small (0.3–1 mm in diam.), subepidermal in origin, soon erumpent; spore mass pulverulent, blackish-brown. – **Teliospores** 37–47(–56) × (32–)37–51 µm (mean 43.5 × 41 µm), mostly composed of 3 cells in typical triangular triplets attached to the pedicel at one tip (rarely 2- or 4-celled, occasionally two or three cells in a row), not or only slightly constricted at septa; each cell with 1 germ pore; wall (pale golden-)brown, evenly 1.5–4 µm thick (mean 2.5 µm), smooth or with a few warts around the germ pores; pedicels hyaline, thin-walled, deciduous. – References: Gäumann (1959: 1212), Lohsomboon et al. (1990b: 218–220), Helfer (2005: 362).

Remarks. The primary uredinia are conspicuous, but *Triphragmium filipendulae* has only been found in Burgenland so far (Poelt and Zwetko 1997: 259). The host plant is present in all provinces of Austria and still common in the Pannonic area (Janchen 1957; Fischer et al. 2008).

2 *Triphragmium ulmariae* (DC.) Link (var. *ulmariae*)

Figs 104, 105a, b

Brachy-form:

0,IIa+b,III on: *Filipendula ulmaria*, (*F. ulmaria* subsp. *denudata*)

Spermatogonia epiphyllous, often nervicolous, subcuticular, flat, reddish-yellow, inconspicuous. – **Primary uredinia** amphigenous, mostly on the petioles or leaf veins, circular to elongated, up to 20 mm long, subepidermal in origin, then erumpent, pulverulent, bright orange-red, causing conspicuous distortions of the leaves, aparaphysate. – **Primary urediniospores** borne singly on pedicels, mostly broadly ellipsoid to subglobose or obovoid, 22–32 × 23–27 µm (mean 28 × 26 µm); wall 1.5–3.5 µm thick (mean 2 µm), hyaline (to pale yellow), echinulate grading to smooth at the base; distance of spines about 3 µm; germ pores obscure; contents orange. – **Secondary uredinia** hypophyllous, scattered, circular, 1 mm in diam., yellow(-brown), aparaphysate (after Lohsomboon et al. 1990b) or surrounded by paraphyses (after Gäumann 1959 and Helfer 2005); paraphyses clavoid, hyaline, 30–50 µm long, 8–15 µm wide. – **Secondary urediniospores** very similar to primary urediniospores but slightly smaller, 23–30 × 20–27(–30) µm (mean 26.5 × 24.5 µm). – **Telia** hypophyllous, small (0.5–2 mm in diam.), scattered or aggregated and confluent, subepidermal in origin, soon erumpent, aparaphysate, sometimes intermixed with urediniospores; spore mass pulverulent, reddish-brown to blackish-brown. – **Teliospores** (35–)39–47(–57) × (33–)38–49(–53) µm (mean 45 × 42 µm), mostly composed of 3 cells (rarely 4), triangular to trigonal-obovoid, not or only slightly constricted at septa; each cell with 1 germ pore; wall (pale) brown, evenly 1.5–4 µm thick (mean 2.8 µm), roughly verrucose, with obtuse warts especially around the germ pores; warts up to 3 µm in diam. and 1 µm high; pedicels hyaline, thin-walled, deciduous. – References: Gäumann (1959: 1210–1211), Lohsomboon et al. (1990b: 221), Helfer (2005: 362–263).

Remarks. At greater altitudes, the secondary uredinia are lacking, and the telia are conspicuously larger (up to 30 mm long), aggregated and confluent. This form has been described as an authentic variety named *Triphragmium ulmariae* var. *alpinum* Lagerh. It differs in possessing telia resembling the primary uredinia in form. These large telia have been found on the nerves and petioles in Germany, Russia and Scandinavia. Similar sori have been found in Scotland at a low elevation, indicating the tendency for micro-forms to evolve under suitable conditions (Wilson and Henderson 1966). Lohsomboon et al. (1990b) did not recognise this form as an authentic variety. – *Triphragmium ulmariae* is quite common in Austria, in contrast to *T. filipendulae* (Poelt and Zwetko 1997: 260).

Xenodochus Schltdl.

The small genus is represented only by the type species in Europe. It is related to *Phragmidium* but differs in the arrangement of the germ pores in the teliospores. Only two species are known, both autoecious on the genus *Sanguisorba*. – **Spermatogonia** intra-epidermal (type 10 according to Cummins and Hiratsuka 2003). – **Aecia**

Figure 104. *Triphragmium ulmariae* on *Filipendula ulmaria*: **a1, a2.** Primary uredinia on deformed leaf veins; **b.** Orange secondary uredinia and blackish telia; **c.** Telia; **d.** Teliospores; (**a** by Julia Kruse; **d** from Poelt and Zwetko 1997: 333).

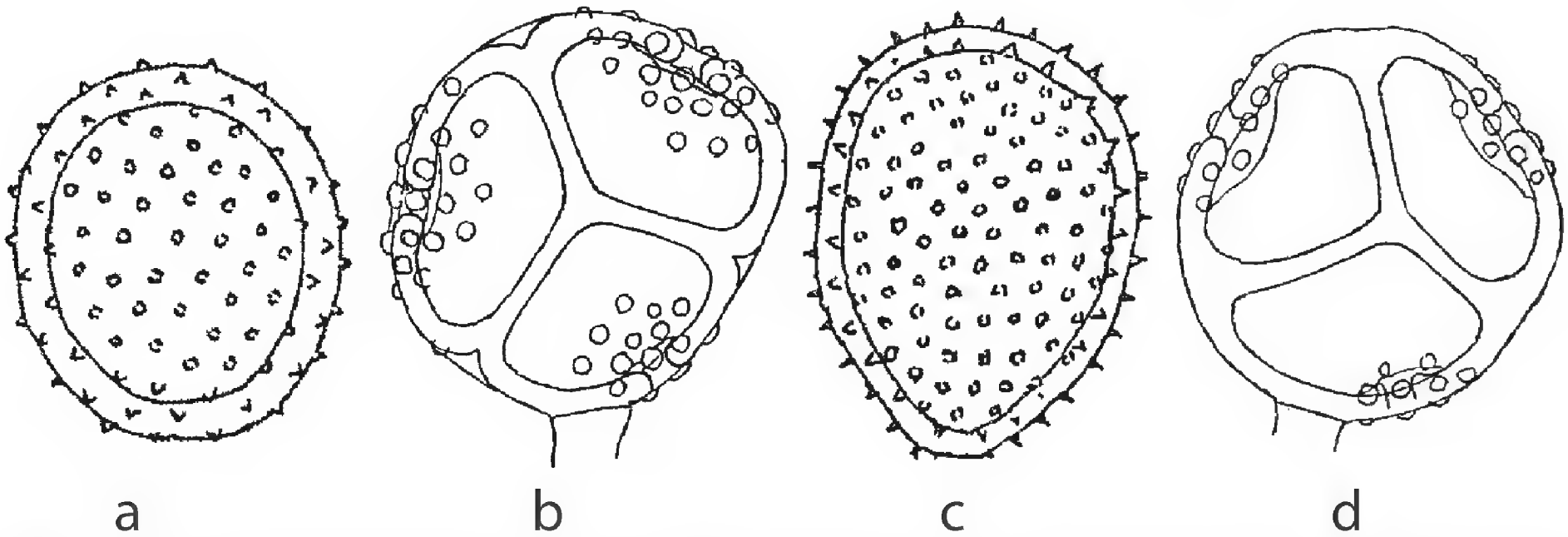


Figure 105. *Triphragmium*. **a, b.** *T. ulmariae* on *Filipendula ulmaria*: **a.** Urediniospore; **b.** Teliospore; **c, d.** *T. filipendulae* on *Filipendula vulgaris*: **c.** Urediniospore; **d.** Teliospore; (**a–d** from Klebahn 1914: 692).

caeomoid with marginal paraphyses, large, subepidermal in origin, erumpent. – **Aeciospores** catenulate; wall hyaline with papillate warts. – Uredinia unknown. – **Telia** subepidermal in origin, erumpent, black. – **Teliospores** borne singly on pedicels, of 3 to many superposed cells; germ pores 2 per cell, opposite, close to the upper septum, except in the end cell which has 1 apical pore; wall smooth, coloured.

1 *Xenodochus carbonarius* Schltdl.

Fig. 106

Syn. *Phragmidium carbonarium* (Schltdl.) G. Winter

Autopsis-form:

0?,I,III on: *Sanguisorba officinalis*

Spermatogonia small, usually not observed. – **Aecia** on yellow or purple leaf spots, mainly hypophyllous on veins, occasionally epiphyllous on petioles and stems, up to 1 cm long, pulverulent, orange; paraphyses 30–62 × 8–16 µm, clavate, yellowish. – **Aeciospores** 17–29 × 13–24 µm (after Helfer 2005), 22.2±1.5 × 19.8±1.8 µm (after Petrova and Denchev 2004), globoid or obovoid; wall 1.5–2 µm thick, hyaline, densely verrucose; warts low, up to 1 µm broad; distance of warts about 1.25 µm; germ pores indistinct; contents orange. – **Telia** amphigenous, often confluent with the aecia, coalescing to compound, strongly convex sori 2–4 mm in diam., soon naked, pulvinate, black. – **Teliospores** up to 300 × 23–30 µm (after Helfer 2005), 155.1±22 × 26.5±1.6 µm (after Petrova and Denchev 2004), elongate-cylindrical, often curved, 3–22-celled, rounded at both ends, strongly constricted, dark-brown; the uppermost cell loosely verrucose with one apical germ pore and a small hyaline papilla; all other cells smooth, with 2 opposite germ pores close to the upper septum; wall brown, in basal cells often nearly hyaline, 1.5–3 µm thick; pedicel short, hyaline, persistent (though somewhat fragile). – References: Gäumann (1959: 1207), Wilson and Henderson (1966: 109, 110), Petrova and Denchev (2004: 113), Helfer (2005: 363).

Remark: Sato and Sato (1980) studied the life cycle by inoculations. They observed repeating aecia ('caeomoid uredinia') and marginal paraphyses. The presence of these paraphyses depends on the maturity of the sori. – According to Helfer et al. (2011) *Xenodochus carbonarius* has suffered decline, irrespective of host plant abundance. For records in Austria see Poelt and Zwetko (1997: 302).

Tranzscheliaceae Aime & McTaggart

The following brief description and comment are cited from Aime and McTaggart (2020): "Spermogonia Group VI (type 7). Aecia aecidium-type; uredinia uredo-type. Teliospores 2-celled, pedicellate, produced from sterile basal cells. Species are macrocyclic and heteroecious, with some derived microcyclic species." … "*Leucotelium* is the sister genus to *Tranzschelia* (Scholler et al. 2019), with which it shares a similar host range and teliospore production from sterile sporogenous cells (Thirumalachar and Cummins [1948], López-Franco and Hennen 1990). Many species of *Tranzschelia* are microcyclic on Ranunculaceae in accordance with Tranzschel's Law (Scholler et al. 2019)".

Leucotelium Tranzschel

In Europe, the small genus is represented only by the type species, *Leucotelium cerasi*. Cummins and Hiratsuka (1983, 2003) placed it as a synonym of *Sorataea*. The teliospores of both genera germinate without dormancy. Many genera of tropical rain forests or other moist climates have narrow, thin-walled and pale teliospores which germinate readily at maturity. Savile (1989) emphasised that this resemblance, which has occurred in many

Figure 106. *Xenodochus carbonarius* on *Sanguisorba officinalis*: **a.** Telia; **b.** Many-celled teliospore; (**b** from Klebahn 1914: 692).

rust lineages, has minimal taxonomic significance. He pointed out that *Leucotelium* is a derivative of *Tranzschelia* with non-resting teliospores, and both are N temperate genera. Like *Tranzschelia*, *Leucotelium* has uredinia and telia on *Prunus* (Rosaceae) and aecia on Ranunculaceae. True *Sorataea* species are restricted to tropical Faboideae.

1 *Leucotelium cerasi* (Castagne) Tranzschel

Figs 107, 108

Syn. *Puccinia cerasi* Castagne; *Mycogone cerasi* Berenger; *Sorataea cerasi* (Castagne) Cummins & Y. Hirats.

Hetereu-form:

0,I on: *Eranthis hyemalis* cult.

II,III on: *Prunus avium*?, *P. domestica*, *P. pumila* var. *depressa* cult., *P. tenella* cult., (*P. armeniaca*, *P. cerasus*, *P. cerasifera*, *P. dulcis*, *P. fruticosa*, *P. padus*, *P. persica*, *P. spinosa*, *P. virginiana*)

Spermatogonia mainly epiphyllous, scattered, subcuticular, sitting on epidermis, orange when young, later on black. – **Aecia** hypophyllous, arising from a systemic mycelium, covering ± the whole leaf surface, subepidermal, erumpent, cupulate, with a broad revolute peridium divided into 4(–5) broad lobes; spore mass orange-brown. Infected leaves are paler (greyish-green) and the petioles are slightly longer; affected plants usually do not flower. – **Aeciospores** produced in chains, 16–26 µm in diam.; wall 1–1.5 µm thick at base, 3 µm at apex, golden orange-brown, densely and finely verrucose, intermixed with larger granules (0.5–1.5 µm in diam.); germ pores indistinct. – **Uredinia** hypophyllous, subepidermal, erumpent, in small, circular or irregular, yellow or reddish leaf spots, aparaphysate; spore mass pale orange-brownish. – **Urediniospores** borne singly on pedicels, 17–30(–35) × 15–20 µm; wall 2 µm thick, pale yellowish brown, echinulate with irregular glabrous patches; germ pores indistinct. – **Telia** hypophyllous, subepidermal, erumpent, in small, circular or irregular, yellow or reddish leaf spots, scattered; the sori look like small, whitish

Figure 107. *Leucotelium cerasi* on *Eranthis hyemalis*: **a.** Infected leaves of a single sterile plant surrounded by lower but fertile uninfected plants; **b.** Young spermatogonia on the upper leaf surface; spermatogonia becoming black when older; **c.** Aecia with white peridia on the lower leaf surface.

Figure 108. *Leucotelium cerasi* on *Prunus tenella*: **a.** Uredinia with pale brownish-orange spore mass on the lower leaf surface; **b.** Mature telia with white bunches of teliospores and basidia.

bunches. – **Teliospores** developing singly from a compact hymenial layer, 30–45 × 15–20 µm, hyaline, 2-celled, slightly constricted; wall 1–2 µm thick, not thickened or only slightly thickened at the apex, hyaline, smooth; pedicels long (up to 40 µm), persistent. – References: Gäumann (1959: 799, sub *Puccinia cerasi*), Helfer (2005: 341).

Remarks. Like in *Tranzschelia* and *Ochropsora*, the mycelium of the aecial stage is perennial in the rhizome of its host plant. *Leucotelium*, *Tranzschelia* and *Ochropsora* produce uredinia and telia on *Prunus*. The uredinia of *Leucotelium* differ from those of *Tranzschelia* and *Ochropsora* by the lack of paraphyses. – In Austria, *Leucotelium cerasi* has been found on *Prunus domestica*, *P. pumila* var. *depressa* cult. and *P. tenella* cult. in the Botanical Garden Graz (Poelt and Zwetko 1997: 70).

Key to the rusts on *Prunus* in Europe

1a Telia hypophyllous, not forming crusts, erumpent. Teliospores stalked, 2-celled. – Uredinia without peridia or palisades of paraphyses, erumpent, pulverulent. Walls of urediniospores pale yellowish-brown or golden-brown 2

1b Telia mainly epiphyllous, forming dark reddish-brown or blackish-brown crusts. Teliospores unstalked, formed within the epidermis cells, divided into (2–)4(–5) cells by anticlinal septa. – Uredinia in purplish to reddish-brown leaf spots, pustular, with a hemispherical peridium, opening with a pore. Urediniospores 15–21(–24) × 10–15 µm, whitish to yellowish(-orange) in mass; walls hyaline ..... *Thekopsora areolata*

1c Basidiosori (telia) hypophyllous, on yellow or red spots, in small, pale whitish-pink crusts, waxy in appearance. Basidia (teliospores) subepidermal, sessile, broadly cylindrical, at first 1-celled, later dividing into 4 cells by horizontal septa, hyaline or pinkish. – Uredinia erumpent, in chlorotic leaf spots, small, whitish to yellowish, surrounded by clavate or incurved paraphyses which form circular cups. Urediniospores 19–28 × 15–25 µm; wall hyaline or very pale brownish, evenly thick ..... *Ochropsora anemones* (syn. *O. ariae*)

2a Telia look like small whitish bunches. Teliospores hyaline, with ± long, persistent pedicels. – Uredinia golden-orange(-brown), without paraphyses. Urediniospores 17–30(–35) × 15–20 µm; wall not thickened at the apex, pale yellowish-brown ..... *Leucotelium cerasi*

2b Telia dark blackish-brown, dusting with age. Teliospores chocolate-brown. Pedicels non-persistent with age. – Uredinia cinnamon-brown, with brown capitate paraphyses intermixed. Urediniospores 20–40(–43) × 10–20 µm; wall thickened at the apex, golden-brown ..... (*Tranzschelia* spp.) 3

3a Teliospores grouped in fascicles with adherent pedicels. The upper spore cell ± globoid; wall chocolate-brown, thickened toward the apex, coarsely verrucose. The lower cell usually narrower, oblong-elliptic; wall almost smooth, pale brown or hyaline ..... *Tranzschelia discolor*

3b Teliospores not grouped in fascicles. Both spore cells ± globoid; walls of both cells chocolate-brown, evenly thick, coarsely verrucose ..... *Tranzschelia pruni-spinosae*

Tranzschelia Arthur

The small genus is represented by five species in Central Europe. The host alternating species produce uredinia and telia on *Prunus* (Rosaceae) and aecia on *Anemone* (Ranunculaceae), the microcyclic species telia on Ranunculaceae. – **Spermatogonia** subcuticular, sitting on epidermis, developing from honey-coloured to black. – **Aecia** subepidermal, erumpent, cupulate, with a broad revolute peridium divided into a few broad lobes; spore mass orange-brown to golden-yellowish. – **Aeciospores** catenulate; wall pigmented, surface evenly verrucose or intermixed with small deciduous plugs. – **Uredinia** subepidermal, erumpent, pulverulent, cinnamon-brown; urediniospores intermixed with capitate paraphyses. – **Urediniospores** borne singly on pedicels; walls echinulate; germ pores equatorial or supraequatorial. – **Telia** subepidermal, erumpent, without paraphyses, dusting with age. – **Teliospores** borne singly on pedicels, usually 2-celled, but 3-celled spores and 1-celled mesospores not uncommon in some species; deeply constricted, spore cells readily separating; wall thick, dark brown (or nearly hyaline), coarsely verrucose (or almost smooth), with 1 germ pore in each cell; pedicels non-persistent with age; in some species teliospores are grouped in fascicles with adherent pedicels, at least in younger telia.

A key for all rust genera and species with uredinia and telia on *Prunus* is attached to *Leucotelium cerasi* (p. 305).

Key to the *Tranzschelia* species in Central Europe

1a Teliospores grouped in fascicles with adherent pedicels; spore mass in young telia seems to consist of small spore balls 2

1b Teliospores not grouped in fascicles; spore mass soon pulverulent 3

2a Facultatively host alternating form with uredinia and telia on *Prunus* spp., and aecia on *Anemone coronaria* and other cultivated *Anemone* spp. ..... *T. discolor*
2b Micro-form with telia on *Pulsatilla* ..... *T. pulsatillae*
2c Micro-form with telia on *Thalictrum* ..... *T. thalictri*
3a Host alternating form with telia on *Prunus* spp. and aecia on *Anemone ranunculoides* ..... *T. pruni-spinosae*
3b Micro-form with telia on other *Anemone* spp. ..... *T. anemones* s.str. (syn. *T. fusca*)

1 *Tranzschelia anemones* (Pers.) Nannf. s.str.

Fig. 109

Syn. *Puccinia anemones* Pers.; ?*Aecidium fuscum* Pers. ex J.F. Gmel.; *Tranzschelia fusca* (Pers.) F. Kern & Thurston; ?*Aecidium fuscum* Relhan; *Puccinia fusca* (Relhan) G. Winter p.p.; *Tranzschelia fusca* (G. Winter) Dietel

Micro-form:

0,III on: *Anemone nemorosa*, *A. trifolia*, (*A. ranunculoides*?)

Spermatogonia epiphyllous or on both sides of the leaves, scattered, dark brown or blackish. – **Telia** hypophyllous, circular, up to 1 mm in diam., crowded and coalescing, arising from a systemic mycelium, ± covering the whole leaf surface. Infected leaves/shoots erect, with longer petioles/stems and smaller leaf segments. Usually, affected plants do not flower or develop imperfect flowers; spore mass soon naked and pulverulent, blackish brown. – **Teliospores** not grouped in fascicles with adherent pedicels, 31–46 × 17–27 µm, deeply constricted and readily breaking at the septum; upper and

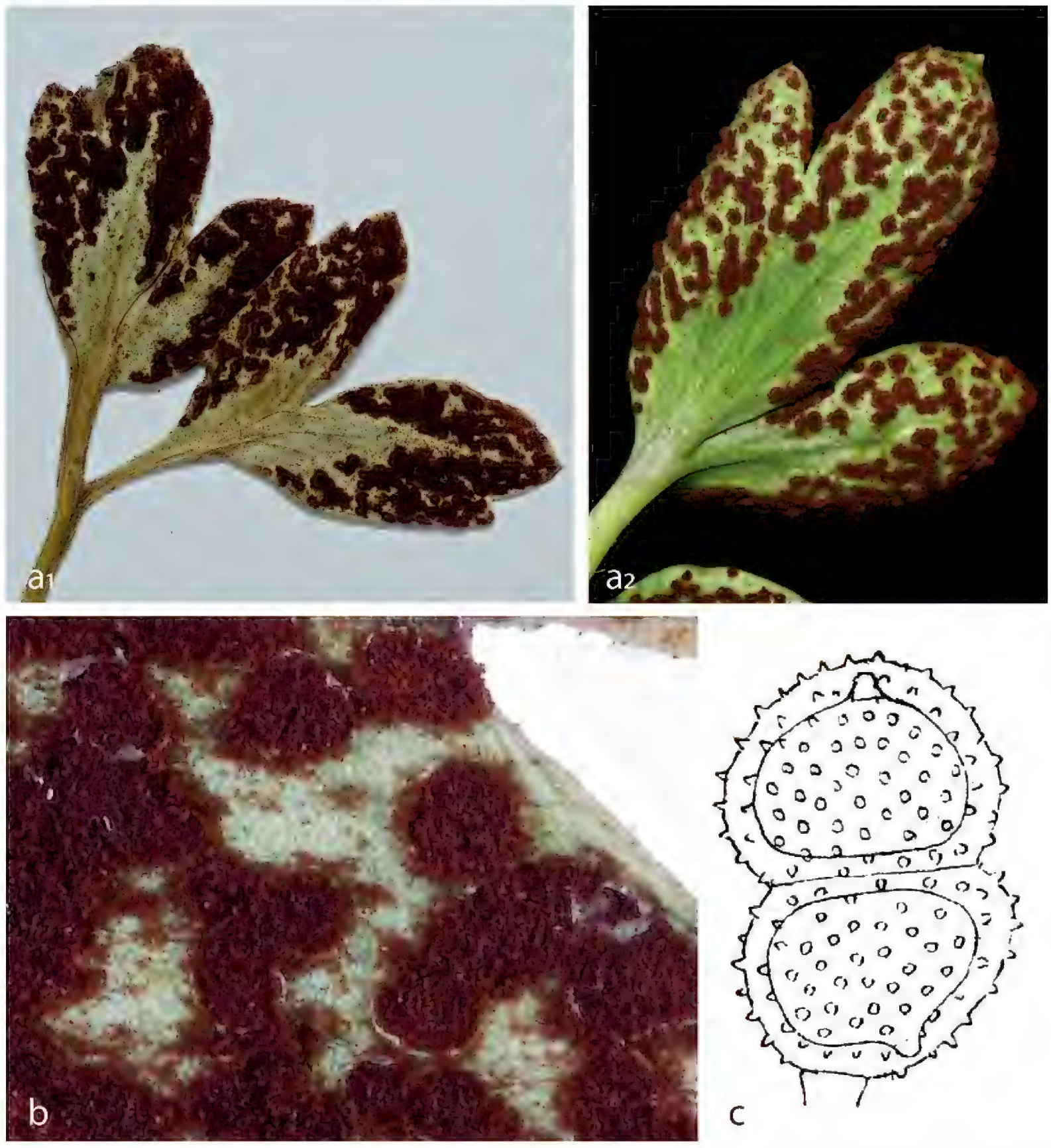


Figure 109. *Tranzschelia anemones* on *Anemone nemorosa*: **a1, a2.** Densely packed telia on deformed shoots/leaves; **b.** Pulverulent spore mass; **c.** Teliospore, both cells of equal size; (**a2** by Walter Obermayer; **c** from Klebahn 1914: 324, as *Puccinia fusca*).

lower cell globoid; wall of both cells chocolate-brown, evenly thick (3 µm), coarsely verrucose; warts pointed; distance of warts 2–3 µm; pedicels hyaline. – References: Gäumann (1959: 205), López-Franco and Hennen (1990: 577–579).

Remarks. López-Franco and Hennen (1990) observed hypha-like, branching paraphyses in the telia. According to Gäumann (1959), *Tranzschelia anemones* does not infect *Anemone ranunculoides*. Records on this host might be due to misidentification of the host plant. Infected plants are deformed and do not flower. – For the distribution of *T. anemones* s.str. in Austria see Poelt and Zwetko (1997: 257, as *T. fusca*).

2 *Tranzschelia* cf. *anemones* (Pers.) Nannf.

Micro-form:

0,III on: *Anemone baldensis*

Morphologically, telia and teliospores on *Anemone baldensis* correspond to the description of López-Franco and Hennen (1990) for *Tranzschelia anemones* (*T. fusca*), i.e., spores are not grouped in fascicles, their walls are rather thin and loosely verrucose. In Austria, *T. anemones* on *Anemone nemorosa* can often be found in colline and submontane altitudinal zones. *Anemone baldensis* is a plant of the alpine zone, therefore its rust might differ biologically from that occurring on *A. nemorosa*. In northern N America several other *Anemone* species can be found as hosts of *T. anemones*. – So far, *Tranzschelia* cf. *anemones* on *Anemone baldensis* is reported from one location only (Poelt and Zwetko 1997: 257, as *T.* cf. *fusca*).

3 *Tranzschelia discolor* (Fuckel) Tranzschel & M.A. Litv.

Figs 110, 111

Syn. *Puccinia discolor* Fuckel; *Tranzschelia pruni-spinosae* (Pers.) Dietel f.sp. *discolor* (Fuckel) E. Fisch.; *T. pruni-spinosae* (Pers.) Dietel var. *discolor* (Fuckel) Dunegan

Hetereu-form (sometimes persisting on the telial host as hemi-form or brachy-form(?), or as anamorphic strains with uredinia only):

0,I on: *Anemone coronaria* cult.

II,III on: *Prunus domestica*, *P. persica*, *P. spinosa*?, (*P. armeniaca*, *P. avium*, *P. cerasifera*, *P. dulcis*, *P. insititia*, *P. mahaleb*, *P. tenella*)

II,[III] on: *Prunus spinosa*, *P. persica*

Spermatogonia on both sides of the leaves, scattered, brown or blackish. – **Aecia** hypophyllous, arising from a systemic mycelium, ± covering the whole surface of hypertrophic leaves; peridium with broad revolute margin split in few lobes; spore mass golden-orange.

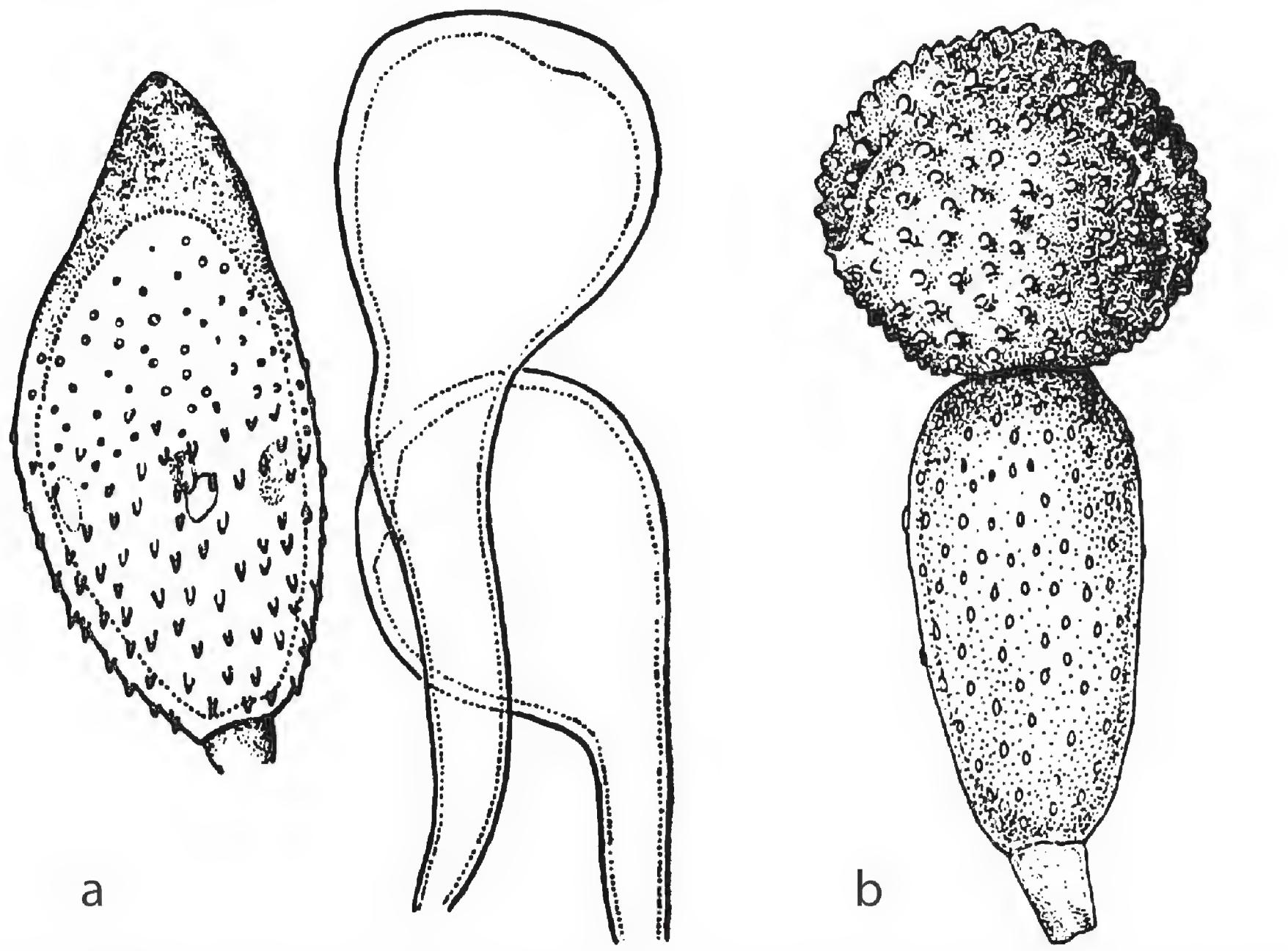


Figure 110. *Tranzschelia discolor* on *Prunus*: **a.** Urediniospore with apically thickened wall and two paraphyses; **b.** Teliospore; the lower cell is narrower and the ornamentation is less distinct; the wall of the upper cell is apically thickened; (**a, b** edited after Viennot-Bourgin 1949: 1119, under *T. pruni-spinosae*, with permission from Elsevier France).

– **Aeciospores** 16–24 µm in diam.; wall golden orange, 1–1.5 µm thick, thickening towards the base up to 2–3 µm (but thickening difficult to discern), finely verrucose with small, deciduous plugs intermixed around the upper two-thirds of the spore surface; germ pores indistinct. – **Uredinia** hypophyllous, seldom amphigenous, in small yellow or brown leaf spots, small, scattered or crowded and coalescing, cinnamon brown; brownish, capitate paraphyses intermixed. – **Urediniospores** 20–40(–43) × 10–19 µm; wall golden brown, 1.5–2 µm thick at sides, 5–9 µm at the apex, echinulate, becoming smooth at the apex; spines larger at the base of the spore; germ pores

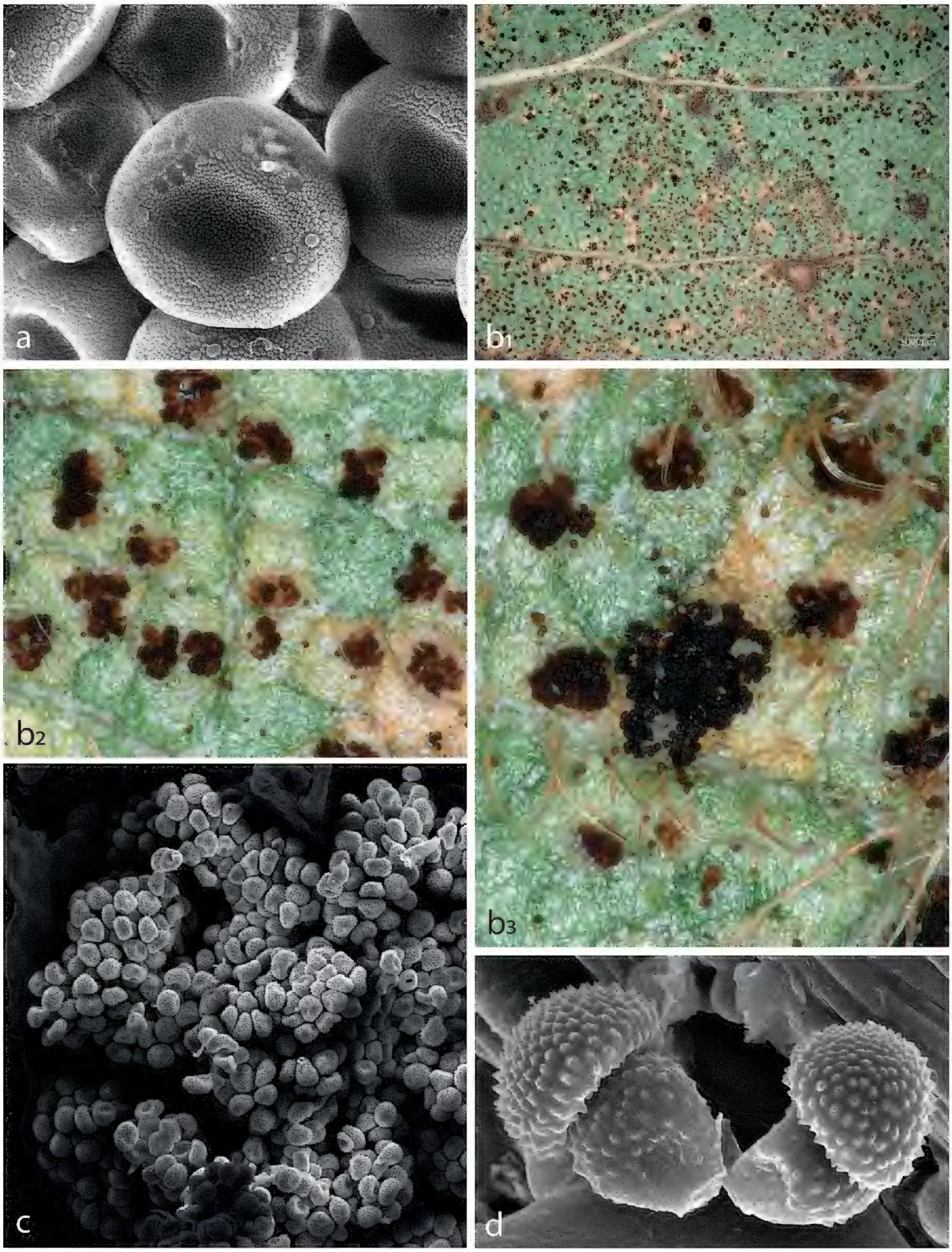


Figure 111. *Tranzschelia discolor*. **a.** On *Anemone coronaria*: aeciospore surface with fine warts and small deciduous plugs in SEM; **b–d.** On *Prunus domestica*: (b1–b3) young telia consisting of distinct spore balls; **c.** Balls of young teliospores in SEM; **d.** Two teliospores in SEM; their lower cells are narrower and longer, and ornamentation is less distinct; (**a, c, d** by Paul Blanz; **b** by Irmgard Krisai-Greilhuber).

3–4, equatorial or supraequatorial. – **Telia** hypophyllous, in small yellow or brown leaf spots, small, circular, at first compact, later pulverulent, blackish brown, 0.25–0.5 mm in diam.; spore mass in young telia consisting of small spore balls. – **Teliospores** grouped in fascicles with adherent pedicels, 30–45 × 18–25 µm, deeply constricted and readily breaking at the septum; upper cell globoid, wall chocolate-brown, thickened toward the apex, coarsely verrucose; lower cell usually narrower, oblong elliptic, wall almost smooth, pale brown or hyaline; pedicels hyaline. – References: Blumer (1963: 107–108), López-Franco and Hennen (1990: 573–575), Helfer (2005: 360).

Remarks. In S Europe, *Prunus persica* and *P. domestica* are more often infected by *Tranzschelia discolor* than in Central Europe. The main distinguishing characters for *T. discolor* and *T. pruni-spinosae* are size, shape, wall pigmentation and ornamentation of the basal cell of the teliospores. According to Blumer (1963), *T. discolor* on *Prunus domestica* can easily be discriminated from *T. pruni-spinosae* even with the naked eye, because telia of *T. discolor* on this host are often surrounded by chlorotic leaf spots. However, these leaf spots also occur when telia of *T. pruni-spinosae* develop on the site of uredinia. Telia produced later are not surrounded by chlorotic spots (see *T. pruni-spinosae*, Fig. 113d, e). Another discriminating character refers to the mass of young teliospores which is conglomerate in *T. discolor* while becoming soon pulverulent in *T. pruni-spinosae*.

Tranzschelia discolor can persist on its telial host as hemi-form or brachy-form(?); some of these strains do not form telia at all, only uredinia, e.g., on *Prunus spinosa* (see also Klenke and Scholler 2015). – For records of *T. discolor* in Austria see Poelt and Zwetko (1997: 256–257).

4 *Tranzschelia pruni-spinosae* (Pers.) Dietel (var. *pruni-spinosae*)

Figs 112, 113

Syn. *Puccinia pruni-spinosae* Pers.; *Tranzschelia pruni-spinosae* (Pers.) Dietel f.sp. *typica* E. Fisch.

Hetereu-form:

0,I on: *Anemone ranunculoides*, (*A. coronaria*?, *A. nemorosa*?, *Hepatica nobilis*?)

II,III on: *Prunus armeniaca*, *P. domestica*, *P. insititia*, *P. pumila* var. *depressa* cult., *P. spinosa*, *P. tenella* cult., (*P. cerasifera*, *P. persica*, *P. virginiana*)

Spermatogonia on both sides of the leaves, scattered, brown or blackish. – **Aecia** hypophyllous, arising from a systemic mycelium, ± covering the whole leaf surface; peridium with broad revolute margin split in few lobes; spore mass (dark) orange-brownish; infected leaves/shoots with longer petioles/stems, usually paler, with smaller leaf segments; affected shoots do not flower or develop imperfect flowers. – **Aeciospores** 16–24 µm in diam.; wall golden orange(-brown), 1–2 µm thick, thickening towards the base (up to 3 µm), evenly verrucose; germ pores indistinct; contents (almost) hyaline. No yellow-orange carotenoid pigments have been found by Zwetko and Pfeifhofer (1991) in fresh spores. – **Uredinia** hypophyllous, seldom amphigenous, small, scattered or crowded and coalescing, (pale) cinnamon brown; abundant brown, capitate paraphyses intermixed. – **Urediniospores** 20–40(–43) × 12–20 µm; wall golden brown, 1.5–2 µm thick at sides, up to 8 µm at the apex, echinulate, becoming smooth at the apex; spines larger at the base of the spore; germ pores 2–5, equatorial to supraequatorial. – **Telia** hypophyllous, scattered or crowded and coalescing, 0.25–0.5 mm in diam.; spore mass soon naked and pulverulent, blackish brown. – **Teliospores** not grouped in fascicles with adherent pedicels, 35–43 × 19–24 µm, deeply constricted and readily breaking at the septum; upper and lower cell globoid; wall of both cells chocolate-brown, evenly thick (1.5–2.5 µm), coarsely verrucose; distance of warts 1–2 µm; pedicels hyaline. – References: Blumer (1963: 107–108), López-Franco and Hennen (1990: 584), Helfer (2005: 361).

Remarks. *Tranzschelia pruni-spinosae* has previously been reported to occur on various host species (in both, aecial and telial stages). Aecia on *Anemone nemorosa* from Germany have been assigned to *T. pruni-spinosae* by Brandenburger (1994), however with reservation. According to Blumer (1963) this rust does not infect *A. nemorosa*. In the aecial stage, distinguishing features for *T. pruni-spinosae* (on *A. ranunculoides*) and *Ochropsora anemones* (syn. *O. ariae*, on *A. nemorosa*) are colour of spore mass, as well as colour and thickness of spore wall (see diagnosis). Thus, identification of both rusts in the aecial stage is easy. But identification of affected plants causes difficulties when *Anemone nemorosa* and *A. ranunculoides* are growing in close vicinity. Both rusts induce similar deformations and inhibit flowering. – From the European part of the former USSR, *Anemone coronaria*, the aecial host of *T. discolor*, has also been reported as host of *T. pruni-spinosae* by Kuprevič and Uljaniščev (1975). *Tranzschelia discolor* differs from *T. pruni-spinosae* by the surface ornamentation of its aeciospores. – *Hepatica nobilis* is listed by Gäumann (1959) as host of *T. pruni-spinosae*, but we do not know his sources in detail. Old records of *T. pruni-spinosae* on *H. nobilis* need to be revised. In N America aecia on *Hepatica* belong to *T. arthurii* (López-Franco and Hennen 1990); in Japan and probably in the Far East provinces of Russia, aecia on *Hepatica* belong to *T. asiatica* (Ono 1994). Dupias (1950) in France noted that neither *A. nemorosa* nor *H. nobilis* showed any symptoms when growing beside infected *A. ranunculoides*. The authors of the present flora observed the same phenomenon in a garden near Graz. – Also some records of the telial stage need to be revised. For instance, *Prunus mahaleb* has been reported as host of *T. arasbaranica* (Abbasi and Scholler 2005), *T. discolor* (Gäumann 1959; Majewski 1977), and *T. pruni-spinosae* (Bontea 1985; Denchev 1995). Several times, we observed healthy peach trees in close vicinity to plum trees which were heavily infected by *T. pruni-spinosae*.

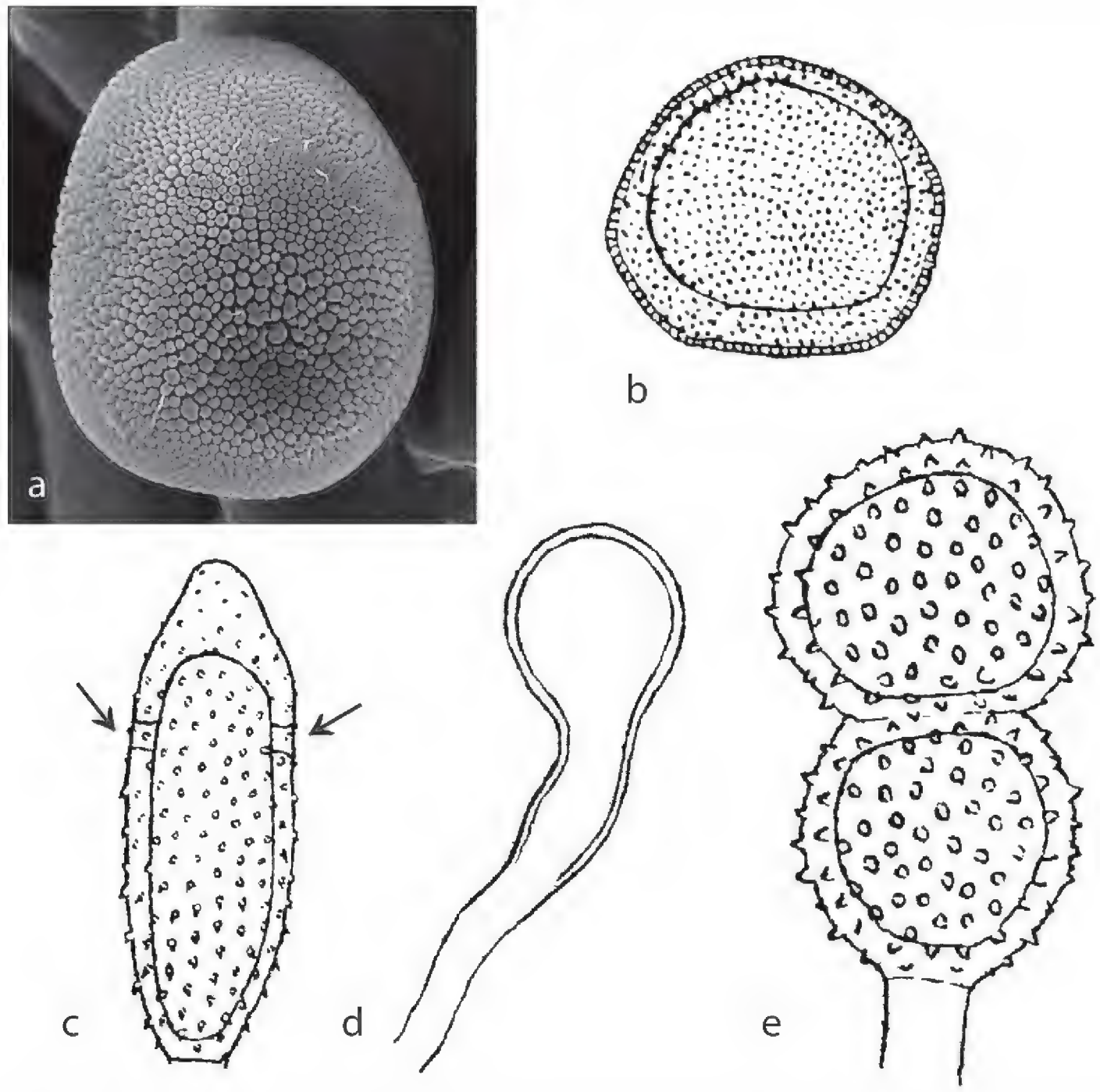


Figure 112. *Tranzschelia pruni-spinosae*. **a, b.** On *Anemone ranunculoides*: **a.** Aeciospore showing evenly verrucose ornamentation in SEM; **b.** Aeciospore with basally thickened wall; **c–e.** On *Prunus domestica*: **c.** Urediniospore with apically thickened wall and supraequatorial germ pores (arrows); **d.** Paraphysis; **e.** 2-celled teliospore, both cells of equal size and ornamentation; (**a** by Paul Blanz; **b–e** from Klebahn 1914: 324, as *Puccinia p.-s.*).

According to Blumer (1963), *P. persica* has been infected by *T. pruni-spinosae* only artificially.

Tranzschelia pruni-spinosae var. *americana* López-Franco & J.F. Hennen (1990) is reported on *Prunus pumila* and *P. pennsylvanica* from N America. *Tranzschelia pruni-spinosae* has been found on *Prunus pumila* var. *depressa* cult. (Scheuer 2003) and *P. tenella* cult. in the Botanical Garden Graz. – For other records of *T. pruni-spinosae* in Austria see Poelt and Zwetko (1997: 257–258).

5 *Tranzschelia pulsatillae* (Opiz) Dietel

Syn. *Puccinia pulsatillae* (Opiz) Rostr. [non Kalchbr.]; *Tranzschelia suffusca* (Holw.) Arthur; *T. anemones* (Pers.) Nannf. p.p.

Micro-form:

[0],III on: *Pulsatilla grandis*, *P. pratensis* subsp. *nigricans*, *P. styriaca*, *P. vernalis*, (*P. vulgaris*)

Spermatogonia epiphyllous, rarely hypophyllous, few and widely scattered, small, brown. – **Telia** hypophyllous, arising from a systemic mycelium, ± covering the whole leaf surface; infected leaves usually with longer petioles and narrower leaf segments; spore mass at first covered by the epidermis, later naked and pulverulent, chocolate-brown. – **Teliospores** grouped in fascicles with adherent pedicels, 31–62 × 15–28 µm, usually deeply constricted; the two cells very variable in size and shape, rarely both cells globoid; lower cell usually longer and narrower; walls evenly thick, yellow-brown, coarsely and densely verrucose; pedicels hyaline. Three-celled teliospores and 1-celled mesospores occur. – References: Gäumann (1959: 206), López-Franco and Hennen (1990: 585–586).

Remarks. López-Franco and Hennen (1990) emphasised that the teliospore pedicels of *Tranzschelia pulsatillae* are greatly elongated. Besides, they observed capitate, peripheral paraphyses.

On the upper side of leaves of *Anemone sylvestris* and *Pulsatilla* species, telia of *Puccinia pulsatillae* Kalchbr. can be found. They are rather large (c. 5 mm in diam.), black pustules covered by the epidermis and surrounded by red leaf spots. In contrast, *Tranzschelia pulsatillae* produces the telia on the lower side of the leaves, with pulverulent spore mass. – For records of *Tranzschelia pulsatillae* in Austria see Poelt and Zwetko (1997: 258), for those of *Puccinia pulsatillae* Kalchbr. see l.c. (162–163).

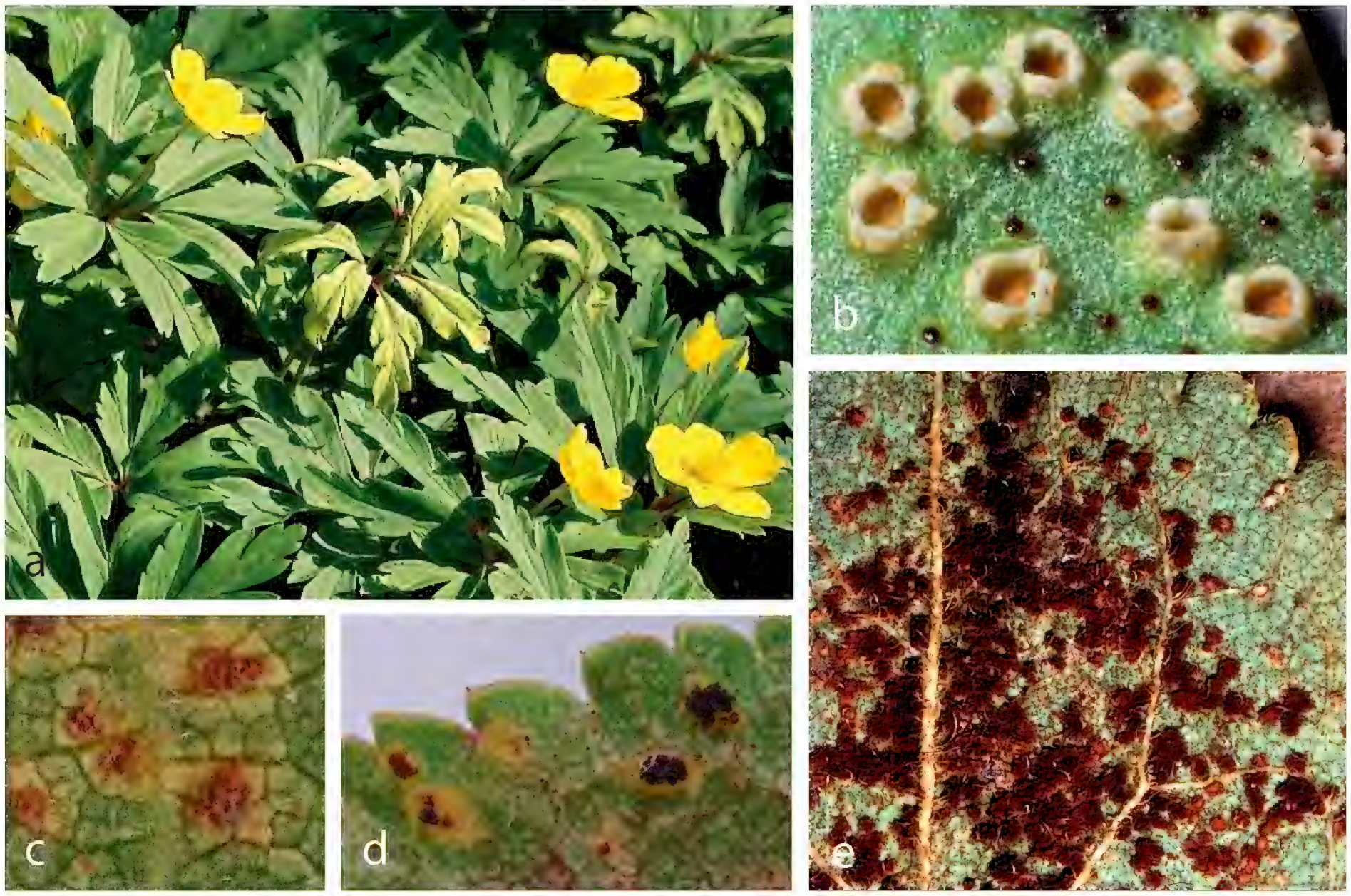


Figure 113. *Tranzschelia pruni-spinosae*. **a, b.** On *Anemone ranunculoides*: **a.** A sterile infected shoot surrounded by lower but flowering uninfected plants; **b.** Spermatogonia (black) and aecia with white peridia and orange spore mass on the lower leaf side; **c–e.** On *Prunus domestica*: **c.** Pulverulent uredinia located on chlorotic spots of the leaf; **d.** First telia replacing uredinia, on chlorotic spots; **e.** Later telia with pulverulent spore mass, not located on chlorotic spots; (**b, e** from Poelt and Zwetko 1997: 332).

6 *Tranzschelia thalictri* (Chevall.) Dietel

Syn. *Tranzschelia anemones* (Pers.) Nannf. p.p.

Micro-form:

(0),III on: *Thalictrum minus*, (*T. aquilegiifolium*, *T. flavum*, *T. foetidum*, *T. morisonii*, *T. simplex*)

Spermatogonia hypophyllous, rarely epiphyllous or sometimes absent, at first light brown, later dark brown. – **Telia** hypophyllous, rarely epiphyllous, circular, 0.5 mm in diam., arising from a systemic mycelium, ± covering the whole leaf surface. Affected plants are usually higher, with longer internodia, smaller and paler leaves, and narrower leaf segments. Mature telia are slightly sunken and surrounded by somewhat thickened host tissue. Spore mass pulverulent, chocolate brown. – **Teliospores** grouped in fascicles with adherent pedicels, (26–)30–40(–55) × (17–)19–24(–29) µm, deeply constricted, variable in size and shape; both cells globoid or lower cell longer and narrower, or both cells long and narrow; wall brown, evenly thick (2–3 µm) except for a ring-like thickening around the germ pore areas, densely verrucose; warts cone-like, rather long; distance of warts 2.5–3 µm; pedicels hyaline. – References: Gäumann (1959: 207–208), López-Franco and Hennen (1990: 585–587).

Remarks. López-Franco and Hennen (1990) observed intermixed, capitate or cylindrical paraphyses and rarely urediniospores in the telia. – See Poelt and Zwetko (1997: 258) for two records of *Tranzschelia thalictri* from Austria.

Genera and species incertae sedis

The genera *Triphragmium*, *Nyssopsora* and *Triphragmiopsis* have been excluded from the Raveneliaceae (Lohsomboon et al. 1990a, b, c). *Triphragmium* is now placed in the Phragmidiaceae (see above). The taxonomic position of *Triphragmiopsis* is still unresolved (Aime and McTaggart 2020). Unfortunately the recent publication placing *Nyssopsora* in a new family Nyssopsoraceae (Yadav et al. 2023) could not be considered in the present treatment anymore.

Nyssopsora Arthur

The small genus is represented only by the type species in Europe. It has three-celled teliospores, and has been included in *Triphragmium* by previous authors. However, it is not related to this genus infecting Rosaceae, which is indicated by the wall ornamentation of its teliospores

(Henderson 1969). Instead, it belongs to a group of rusts parasitising Araliaceae and other families. It is mainly distributed in E and SE Asia (see Lohsomboon et al. 1990a). *Nyssopsora* differs from *Triphragmium* in the number of germ pores in the teliospore cells; the former has two or three, the latter only one. *Triphragmiopsis* and *Nyssopsora* differ in shape and ontogeny of the teliospore wall ornamentation; *Triphragmiopsis* has a verrucose wall, while *Nyssopsora* has a wall with conspicuous projections. As already mentioned above, Yadav et al. (2023) recently placed *Nyssopsora* in a new family Nyssopsoraceae Sanjay & Raghv. Singh.

1 *Nyssopsora echinata* (Lév.) Arthur

Fig. 114

Syn. *Triphragmium echinatum* Lév.

Micro-form:

III on: *Mutellina adonidifolia* [syn. *Ligusticum mutellina*], (*Meum athamanticum*)

Spermatogonia lacking. – **Telia** amphigenous and on the petioles, also on stems and fruits, rounded or elongated, at first small but soon becoming confluent, and then forming pustules on the petioles up to 20 mm long, subepidermal in origin, soon erumpent, surrounded by the conspicuous, ruptured epidermis; spore mass pulverulent, black. – **Teliospores** 29–42 × 27–40 µm (mean 34 × 32 µm), composed of three cells, one basal pedicellate cell and two apical cells, trigonal-obovoid, slightly constricted at septa; wall blackish-brown, evenly 1–3 µm thick, with conspicuous, slightly curved, spine-like projections, some sharply pointed and others with minute, dichotomous branches at the ends, brown but paler at the apex, 4–18 µm long, 2–3 µm thick; each cell with 2(–4) germ pores, which are situated near the inner angles; pedicels hyaline, ± deciduous. – References: Gäumann (1959: 1215), Wilson and Henderson (1966: 114), Lohsomboon et al. (1990a: 910).

Remarks. *Nyssopsora echinata* causes some swelling and distortion on the stems and petioles. Its telia resemble the sori of some smut fungi in appearance (e.g., *Urocystis* species). – For records of *N. echinata* in Austria see Poelt and Zwetko (1997: 91).

Triphragmiopsis Naumov

The small genus is represented by only one species in Europe. Two further species occur in E Asia. Their host range is rather uncommon. The type species produces aecia and telia on *Jeffersonia* (Podophyllaceae), while the telial host of the second species in Asia is *Larix* (Pinaceae); the microcyclic European species occurs on *Isopyrum* (Ranunculaceae). The genera *Triphragmiopsis*, *Triphragmium* and *Nyssopsora* are characterised by 3-celled teliospores. *Triphragmiopsis* differs from *Triphragmium* in the number of germ pores per teliospore cell; the former has two or three, the latter only one. *Triphragmiopsis* differs from *Nyssopsora* in shape and ontogeny of the teliospore wall ornamentation; the former has a verrucose wall, the latter has a wall with conspicuous projections.

1 *Triphragmiopsis isopyri* (Moug. & Nestl.) Tranzschel

Fig. 115

Syn. *Triphragmium isopyri* Moug. & Nestl.; *Nyssopsora isopyri* (Moug. & Nestl.) T. Majewski

Micro-form:

III on: *Isopyrum thalictroides*

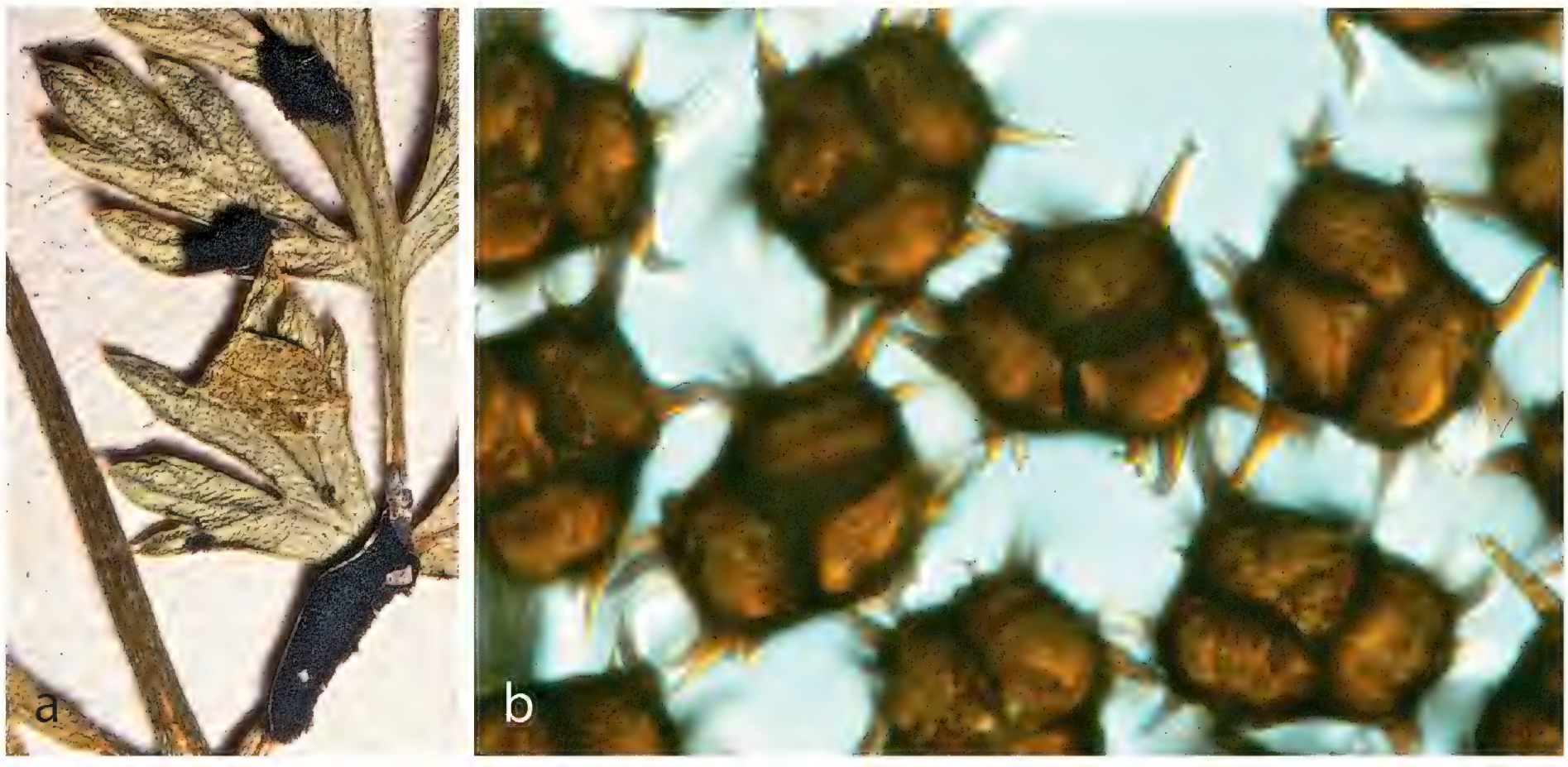


Figure 114. *Nyssopsora echinata* on *Mutellina adonidifolia*: **a.** Telia on petioles and lower side of the leaves with pulverulent black spore mass; **b.** 3-celled teliospores with spine-like projections; (**a, b** from Poelt and Zwetko 1997: 333).

Figure 115. *Triphragmiopsis isopyri* on *Isopyrum thalictroides*: **a.** Telia with pulverulent spore mass and fragments of torn epidermis; **b.** 3-celled teliospores; (**b** from Poelt and Zwetko 1997: 333).

Spermatogonia lacking. – **Telia** amphigenous, also on petioles, rounded or irregularly elongated (0.3–1 mm in diam.), aggregated in groups up to 10 mm long; subepidermal in origin, first swollen then erumpent, without paraphyses, arising from a ± systemic mycelium. Affected plants usually do not flower. Spore mass pulverulent, chocolate brown. – **Teliospores** mostly triangular or ellipsoid, sometimes irregular in shape, 39–57 × 29–47 µm (mean 46.5 × 40.5 µm); composed of three cells, one basal pedicellate cell and two apical cells, not or only slightly constricted at septa; wall yellowish-brown to cinnamon-brown, evenly 1.5–4 µm thick (mean 2.5 µm), loosely verrucose, with 2–3 germ pores in each cell; pedicels hyaline, non-persistent. – References: Gäumann (1959: 1214), Lohsomboon et al. (1990c: 340–341).

Remarks. *Triphragmiopsis isopyri* is a very rare species in Central Europe, but recorded from W, E and SE Europe. – See Poelt and Zwetko (1997: 259) for a record of *T. isopyri* from Austria.

***Uredo* auct.**

In a traditional sense, the anamorphic taxon *Uredo* includes the uredinial stages of various teleomorphic rust genera, e.g., *Puccinia-Uromyces*, *Pucciniastrum* s.l., *Melampsora*, *Cronartium*. The assignment of the following two rusts to a perfect taxon raises questions.

1 *Uredo alpestris* J. Schröt.

Life cycle insufficiently known:

II on: *Viola biflora*

Spermatogonia, aecia and telia wanting. – Uredinia of two kinds: **Uredinia** produced in summer are hypophyllous, scattered, very small (0.1–0.15 mm in diam.), round or elongated, often closely grouped, at first covered by the epidermis, soon naked, orange; peridium lacking. – **Urediniospores** 21–28 × 10–14 µm, broadly fusiform, apically ending in a mucro-like point about 5 µm long; wall 1 µm thick or less, hyaline, smooth; germ pores obscure; contents golden-yellow. – **Uredinia** produced in autumn (amphisporic sori) partly resembling the uredinia produced in summer, but larger (up to 1 mm), long covered by the epidermis, surrounded by low paraphyses. – **Urediniospores** of the second kind (amphispores) ellipsoid, not ending in a mucro-like point; wall 1.2–1.5 µm thick, slightly thicker at the apex, hyaline; wall surface irregularly rugged ('buckelig' after Gäumann 1959; 'fein gezähnelt bis wellig' after Berndt 1993). – For transmission electron micrographs of wall ornamentation and pedicels of the urediniospores see Berndt (1993). – Reference: Gäumann (1959: 19).

Remarks. Contrary to the urediniospores of *Puccinia violae* s.l., both kinds of spores of *Uredo alpestris* lack wall pigmentation. Due to the occurrence of amphispores, this rust which is common in the Alps was put close to the fern inhabiting rust genus *Uredinopsis* by Dietel (1916) and Gäumann (1959). However, on the basis of haustorial markers Berndt (1993) did not believe in an affiliation of *Uredo alpestris* to *Uredinopsis* or another rust genus on ferns. There is no sign of a peridium in *Uredo alpestris*, which would be typical for the uredinia of fern rusts. Also, molecular data place *Uredo alpestris* distant from the fern rusts (Maier et al. 2003). Ono (1980) believes that the 'amphispores' may belong to another rust, but his supposition is inconsistent with the observation that both kinds of urediniospores can occur in old sori of the first kind (Dietel 1916). – For the distribution of *Uredo alpestris* in Austria see Poelt and Zwetko (1997: 304).

(2) *Uredo colchici-autumnalis* A.L. Guyot & Massenot

Life cycle insufficiently known:

(0?,II on: *Colchicum autumnale*)

The presence of hypophyllous spermatogonia remains uncertain. – **Uredinia** epiphyllous on roundish leaf spots, in circular disposition, minute, 0.5–1 mm in diam., 0.2–0.3 mm high, pustular, opening with a pore; peridium delicate, hemispherical; outer walls of peridial cells 6–8 µm thick, striate; inner walls 3–4 µm thick, not striate. – **Urediniospores** subgloboid to ovoid, (18–)19–23(–29) × (15–)17–20(–21) µm, mean 20.8 × 18.7 µm; wall 1–2 µm thick, yellowish to brownish, finely and densely verrucose, with 5–8 distinct germ pores. – Reference: Guyot and Massenot (1958: 497–499).

Remarks. According to Guyot and Massenot (1958), this taxon belongs to the genus *Uredo*. These authors remarked that its spores are not disposed in chains inside the sori, but they neither described nor drew spore pedicels. Savile (1979) emphasised that there have been claims of sessile urediniospores in a few inadequately studied genera, but no such claims can be accepted unless based on cytological preparations from fresh material. The delicate pedicels in many genera with uredinial peridia are difficult to recognise in herbarium material. Unless fresh material is studied, it remains uncertain if the spores of *Uredo colchici-autumnalis* can be interpreted as pedicellate urediniospores or catenulate aeciospores. Due to the presence of vestiges of a peridium, this rare rust was supposed to be close to *Pucciniastrum* and related genera. However, the walls of aecio- and urediniospores of these genera lack pigmentation, but the spore walls of *Uredo colchici-autumnalis* are pigmented. On the basis of this character, we do not believe in an affiliation of *Uredo colchici-autumnalis* to *Pucciniastrum*, e.g., to *Pucciniastrum goodyerae* (a parasite of the orchid *Goodyera*). Gäumann (1959) discussed *Uredo colchici-autumnalis* in the appendix of his 'Formenkreis' of *Uromyces scillarum*. – Poelt and Zwetko (1997) do not mention *Uredo colchici-autumnalis* which has been described from S France (Guyot and Massenot 1958; Gäumann 1959).

References

Abbasi M, Scholler M (2005) A new species of *Tranzschelia* (Uredinales) on Prunus mahaleb. Sydowia 57: 149–153.

Aime MC (2006) Toward resolving family-level relationships in rust fungi (Uredinales). Mycoscience 47: 112–122. https://doi.org/10.1007/S10267-006-0281-0

Aime MC, McTaggart AR (2020) A higher-rank classification for rust fungi, with notes on genera. Fungal Systematics and Evolution 7[2021]: 21–47. https://doi.org/10.3114/fuse.2021.07.02

Aime MC, Bell CD, Wilson AW (2018a) Deconstructing the evolutionary complexity between rust fungi (Pucciniales) and their plant hosts. Studies in Mycology 89: 143–152. https://doi.org/10.1016/j.simyco.2018.02.002

Aime MC, Castlebury LA, Abbasi M, Begerow D, Berndt R, Kirschner R, Marvanová L, Ono Y, Padamsee M, Scholler M, Thines M, Rossman AY (2018b) Competing sexual and asexual generic names in Pucciniomycotina and Ustilaginomycotina (Basidiomycota) and recommendations for use. IMA Fungus 9(1): 75–90. https://doi.org/10.5598/imafungus.2018.09.01.06

Arthur JC (1905) Terminology of the spore-structures in the Uredinales. The Botanical Gazette 39: 218–221. https://doi.org/10.1086/328608

Arthur JC (1906) Eine auf die Struktur und Entwicklungsgeschichte begründete Klassifikation der Uredineen. Résultats scientifiques du Congrès International de Botanique Vienne 1905, 331–348.

Arthur JC [et al.] (1907–1927) Order Uredinales. In: North American Flora 7, Parts 2–12: 83–848. [Host index by Dorothy May White (1931), Part 13: 849–969]. The New York Botanical Garden, New York.

Arthur JC (1912) Order Uredinales. Aecidiaceae (continuatio). In: North American Flora 7, Part 3: 161–187, 211–268. The New York Botanical Garden, New York.

Arthur JC (1917) Relationship of the genus *Kuehneola*. Bulletin of the Torrey Botanical Club 44: 501–511. https://doi.org/10.2307/2479504

Arthur JC (1925) Terminology of the Uredinales. The Botanical Gazette 80: 219–223. https://doi.org/10.1086/333526

Arthur JC, [in collaboration with] Kern FD, Orton CR, Fromme FD, Jackson HS, Mains EB, Bisby GR (1929) The Plant Rusts (Uredinales). J. Wiley & Sons, New York, 446 pp.

Arthur JC (1932) Terminologie der Uredinales. Berichte der Deutschen Botanischen Gesellschaft 50a: 24–27. https://doi.org/10.1111/j.1438-8677.1932.tb03818.x

Arthur JC (1934) Manual of the Rusts in United States and Canada. Purdue Research Foundation, Lafayette, Ind., [XV +] 438 pp.

Arthur JC, Cummins GB (1962) Manual of the rusts in United States and Canada. Illustrations and a new supplement by Professor George B. Cummins. Hafner Publishing Company, New York, [XV +] 438 pp.[, supplement pages 1A–23A].

Azbukina ZM (1974) Rzhavchinnyye griby Dalnego Vostoka. Izdatel'stvo "Nauka", Moskva, 528 pp.

Barrès B, Halkett F, Dutech C, Andrieux A, Pinon J, Frey P (2008) Genetic structure of the poplar rust fungus *Melampsora larici-populina*: Evidence for isolation by distance in Europe and recent founder effects overseas. Infection, Genetics and Evolution 8: 577–587. https://doi.org/10.1016/j.meegid.2008.04.005

Bauer R, Oberwinkler F (1986) Experimentell-ontogenetische und karyologische Untersuchungen an *Ochropsora ariae*. Zeitschrift für Mykologie 52: 271–275.

Bedlan G (1984) Die Gattung *Phragmidium* Link mit besonderer Berücksichtigung des Formenkreises um *Phragmidium mucronatum* und *Phr. potentillae* in Mitteleuropa. Pflanzenschutzberichte 46: 33–60.

Beenken L, Lutz M, Scholler M (2017) DNA barcoding and phylogenetic analyses of the genus *Coleosporium* (Pucciniales) reveal that the North American goldenrod rust *C. solidaginis* is a neomycete on introduced and native *Solidago* species in Europe. Mycological Progress 16: 1073–1085. https://doi.org/10.1007/s11557-017-1357-2

Berndt R (1993) Untersuchungen zur Ultrastruktur und Anatomie der Melampsoraceen (Uredinales, Basidiomycetes). Dissertation, Eberhard-Karls-Universität Tübingen, 239 pp.

Berndt R (1996) Ultrastructure of the D-haustoria of *Coleosporium* spp. (rust fungi, Uredinales). Sydowia 48: 263–272.

Berndt R (1999a) Neufunde von Rostpilzen in Baden-Württemberg. Carolinea 57: 57–64.

Berndt R (1999b) *Chrysomyxa* rust: morphology and ultrastructure of D-haustoria, uredinia, and telia. Canadian Journal of Botany 77: 1469–1484. https://doi.org/10.1139/cjb-77-10-1469

Berndt R (2008) The rust fungi (Uredinales) on ferns in South Africa. Mycological Progress 7: 7–19. https://doi.org/10.1007/s11557-007-0548-7

Berndt R, Brodtbeck T (2020) Checklist and host index of the rust fungi (Uredinales) of Switzerland. https://doi.org/10.3929/ethz-b-000418925

Berndt R, Oberwinkler F (1995) Ultrastructure of the parasitic interface of *Pucciniastrum*, *Thekopsora*, *Naohidemyces* and *Calyptospora* (Uredinales, Pucciniastraceae) in the dikaryotic stage. Mycoscience 36: 51–59. https://doi.org/10.1007/BF02268573

Berndt R, Oberwinkler F (1997) Haustorial ultrastructure and morphology of *Melampsorella* and *Thekopsora areolata*. Mycologia 89: 698–705. https://doi.org/10.1080/00275514.1997.12026835

Berndt R, Bauer R, Oberwinkler F (1994) Ultrastructure of host-parasite interface in the fern rusts *Milesia*, *Uredinopsis* and *Hyalopsora* (Pucciniastraceae, Uredinales). Canadian Journal of Botany 72: 1084–1094. https://doi.org/10.1139/b94-133

Blanz P, Zwetko P[†] (2018) Remarks on species concepts in European Florae of Rust Fungi. In: Blanz P (Ed.) Biodiversity and Ecology of Fungi, Lichens, and Mosses. Kerner von Marilaun Workshop 2015 in memory of Josef Poelt. Biosystematics and Ecology Series 34. Verlag der Österreichischen Akademie der Wissenschaften, Wien, 271–287. https://doi.org/10.1553/0x003892e7

Blumer S (1963) Rost- und Brandpilze auf Kulturpflanzen. Ein Bestimmungsbuch für die in Mitteleuropa vorkommenden Arten. G. Fischer, Jena, 379 pp.

Boerema GH, Verhoeven AA (1972) Check-list for scientific names of common parasitic fungi. Series 1a: Fungi on trees and shrubs. Netherlands Journal of Plant Pathology 78(Suppl. 1): 1–55. https://doi.org/10.1007/BF01976689

Bontea V (1985) Ciuperci Parazite şi Saprofite din România. I. Editura Academiei Republicii Socialiste România, Bucureşti, 590 pp.

Brandenburger W (1963) Vademecum zum Sammeln parasitischer Pilze mit besonderer Berücksichtigung der in Mitteleuropa vorkommenden Uredinales, Ustilaginales, Erysiphales, Taphrinales und Peronosporales. Eugen Ulmer, Stuttgart, 186 pp.

Brandenburger W (1985) Parasitische Pilze an Gefäßpflanzen in Europa. Gustav Fischer Verlag, Stuttgart, New York, [XXI +] 1248 pp.

Brandenburger W (1994) Die Verbreitung der in den westlichen Ländern der Bundesrepublik Deutschland beobachteten Rostpilze (Uredinales). Eine Bestandsaufnahme nach Literaturangaben. Regensburger Mykologische Schriften 3. Verlag der Regensburgischen Botanischen Gesellschaft, Regensburg, 381 pp.

Brandenburger W (1995) Ein Beitrag zur Pilzflora des Wallis. Bulletin de la Murithienne, Société Valaisanne des Sciences Naturelles 113: 129–145.

Brandenburger W (1996) Ein Beitrag zur Pilzflora des Berner Oberlandes. Mycologia Helvetica 8: 3–41.

Brandenburger W (1997a) Beiträge zur Pilzflora Graubündens. I. Mehltau-, Rost- und Brandpilze aus der Lumnezia/Bündner Oberland. Mycologia Helvetica 9: 39–70.

Brandenburger W (1997b) Beiträge zur Pilzflora Graubündens. II. Mehltau-, Rost- und Brandpilze aus der Val Fenga (Fimbertal). Mycologia Helvetica 9: 71–77.

Braun U (1981) Vorarbeiten zu einer Rostpilzflora der DDR. Feddes Repertorium 92: 95–123. https://doi.org/10.1002/fedr.19810920105

Braun U (1982) Die Rostpilze (Uredinales) der Deutschen Demokratischen Republik. Feddes Repertorium 93: 213–333. https://doi.org/10.1002/fedr.19820930303

Braun U, Bensch K (2022) (2891) Proposal to conserve the name *Puccinia psidii* (*Austropuccinia psidii*) against *Caeoma eugeniarum* and *Uredo neurophila* (Basidiomycota: Pucciniaceae). Taxon 71: 687–688. https://doi.org/10.1002/tax.12745

Bubner B, Buchheit R, Friedrich F, Kummer V, Scholler M (2019) Species identification of European forest pathogens of the genus *Milesina* (Pucciniales) using urediniospore morphology and molecular barcoding including *M. woodwardiana* sp. nov. MycoKeys 48: 1–40. https://doi.org/10.3897/mycokeys.48.30350

Buczacki ST, Harris KM (1981) Collins guide to the pests, diseases and disorders of garden plants. Collins, London, 512 pp.

Butin H (1989) Krankheiten der Wald- und Parkbäume. Diagnose - Biologie - Bekämpfung. 2. Auflage. Georg Thieme Verlag, Stuttgart, New York, [X +] 216 pp.

Ciszewska-Marciniak J, Jedryczka M (2011) Life cycle and genetic diversity of willow rusts (*Melampsora* spp.) in Europe. Acta Agrobotanica 64: 3–10. https://doi.org/10.5586/aa.2011.001

Ciszewska-Marciniak J, Jedryczka M, Jeżowski S, Przyborowski J, Wojciechowicz K, Zenkteler E (2010) Morphology of uredinia and urediniospores of the fungus *Melampsora larici-epitea* Kleb. a damaging pathogen of common osier (*Salix viminalis* L.) in Poland. Acta Agrobotanica 63: 117–125. https://doi.org/10.5586/aa.2010.039

Colley RH (1918) Parasitism, morphology and cytology of *Cronartium ribicola*. Journal of Agricultural Research (Washington DC) 15: 619–659.

Crane PE (2000) Systematics and biology of the genus *Chrysomyxa* (Uredinales). PhD thesis Univ. Alberta, Edmonton, 249 pp.

Crane PE (2001) Morphology, taxonomy, and nomenclature of the *Chrysomyxa ledi* complex and related rust fungi on spruce and Ericaceae in North America and Europe. Canadian Journal of Botany 79: 957–982. https://doi.org/10.1139/b01-071

Crane PE, Hiratsuka Y, Currah RS (2000) Clarification of the life-cycle of *Chrysomyxa woroninii* on *Ledum* and *Picea*. Mycological Research 104: 581–586. https://doi.org/10.1017/S0953756299001677

Cummins GB (1936) Phylogenetic significance of the pores in urediospores. Mycologia 28: 103–132. https://doi.org/10.1080/00275514.1936.12017122

Cummins GB (1959) Illustrated genera of rust fungi. Burgess Publishing Company, Minneapolis, 131 pp.

Cummins GB (1971) The rust fungi of cereals, grasses and bamboos. Springer, Berlin, Heidelberg, New York, 570 pp. https://doi.org/10.1007/978-3-642-88451-1

Cummins GB (1978) Rust fungi on legumes and composites in North America. University of Arizona Press, Tucson, 424 pp.

Cummins GB, Hiratsuka Y (1983) Illustrated Genera of Rust Fungi. Revised Edition. The American Phytopathological Society, St. Paul, Minnesota, [V +] 152 pp.

Cummins GB, Hiratsuka Y (2003) Illustrated Genera of Rust Fungi. Third edition. APS Press, St. Paul, Minn., [IX +] 225 pp.

De Bary HA (1865) Neue Untersuchungen über die Uredineen, insbesondere über die Entwickelung der *Puccinia graminis* und der Zusammenhang derselben mit *Aecidium berberidis*. Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1865: 15–49.

De Bary HA (1866) Morphologie und Physiologie der Pilze, Flechten und Myxomyceten. Verlag von Wilhelm Engelmann, Leipzig, [XII +] 316 pp. https://doi.org/10.5962/bhl.title.120970

De Candolle AP (1807) Rapport sur un Voyage botanique et agronomique dans les Départemens de l'Ouest. Mémoires d'agriculture, d'économie rurale et domestique, pub. par la Société d'Agriculture du Département de la Seine 10: 228–292.

De Candolle AP (1815) Flore française. Volume 6. Desray, Paris, 662 pp.[, pl. I–XI.]

Denchev CM (1995) Bulgarian Uredinales. Mycotaxon 55: 405–465.

Diedicke H (1910) Aufzählung der in der Umgebung Erfurts beobachteten Micromyceten. Jahrbücher der königlichen Akademie gemeinnütziger Wissenschaften zu Erfurt 36: 123–172.

Dietel P (1895) Zur Kenntnis der Gattung *Uredinopsis* Magn. Berichte der Deutschen Botanischen Gesellschaft 13: 326–332[, 1 Tafel]. https://doi.org/10.1111/j.1438-8677.1895.tb04662.x

Dietel P (1905) Über die Arten der Gattung *Phragmidium*. Hedwigia 44: 112–132, 330–346.

Dietel P (1916) Über die systematische Stellung von *Uredo alpestris* Schröt. Annales Mycologici 14: 98–99.

Dietel P (1927) Über *Phragmidium rubi* (Pers.) Wint. var. *candicantium* Vleugel. Annales Mycologici 25: 474–477.

Dietel P (1928) Unterklasse Hemibasidii (Ustilaginales und Uredinales). In: Engler A (Ed.) Die natürlichen Pflanzenfamilien. Zweite Auflage, 6. Band. Verlag von Wilhelm Engelmann, Leipzig, 1–98.

Dupias G (1950) Étude expérimentale d'Urédinées hétéroxènes (Troisième note). Bulletin de la Société d'Histoire Naturelle de Toulouse 85: 33–44.

Dupias G (1967) Quelques Urédinées du Massif Central français. Uredineana 6 (= Encyclopédie Mycologique XXXIV) (1965): 517–530.

Durrieu G (1979) Les cycles des Urédinales. Problèms de terminologie. Bulletin de la Société Mycologique de France 95: 379–392.

Engelke C (1900) Beitrag zur hannoverschen Pilzflora. 48./49. Jahresbericht der Naturhistorischen Gesellschaft zu Hannover (1897/98–1898/99): 80–126.

Epstein L, Buurlage MB (1988) Nuclear division in germinating aeciospores and its taxonomic significance for the western gall rust fungus, *Peridermium harknessii*. Mycologia 80: 235–240. https://doi.org/10.1080/00275514.1988.12025525

Faull JH (1932) Taxonomy and geographical distribution of the genus *Milesia*. Contributions from the Arnold Arboretum of Harvard University 2. Published by the Arnold Arboretum of Harvard University, Jamaica Plain, Mass., U.S.A., 138 pp.[, 9 plates.]

Faull JH (1938a) Taxonomy and geographical distribution of the genus *Uredinopsis*. Contributions from the Arnold Arboretum of Harvard University 11. Published by the Arnold Arboretum of Harvard University, Jamaica Plain, Mass., U.S.A., 120 pp.[, 6 plates.]

Faull JH (1938b) The biology of rusts of the genus *Uredinopsis*. Journal of the Arnold Arboretum 19: 402–436. https://doi.org/10.5962/p.324594

Feau N, Vialle A, Alaire M, Tanguay P, Joly DL, Frey P, Callan BE, Hamelin RC (2009) Fungal pathogen (mis-)identifications. A case study with DNA barcodes on *Melampsora* rusts of aspen and white poplar. Mycological Research 113: 713–724. https://doi.org/10.1016/j.mycres.2009.02.007

Feau N, Vialle A, Alaire M, Maier W, Hamelin RC (2011) DNA barcoding in the rust genus *Chrysomyxa* and its implications for the phylogeny of the genus. Mycologia 103: 1250–1266. https://doi.org/10.3852/10-426

Ferrada EE, Böhm L, Montenegro O, Llancao M, Romero C, Briceño EX, Morales RA, Díaz GA (2020) First Report of Leaf Rust of *Fuchsia magellanica* Caused by *Pucciniastrum circaeae* in Valdivia, Chile. Plant Disease 104: 1548. https://doi.org/10.1094/PDIS-11-19-2356-PDN

Fischer E (1904) Die Uredineen der Schweiz. Beiträge zur Kryptogamenflora der Schweiz 2(2), [XCIV +] 591 pp. Verlag von K. J. Wyss, Bern.

Fischer E (1910) Studien zur Biologie von *Gymnosporangium juniperinum*. 2. Mitteil. Zeitschrift für Botanik (Jena) 2: 753–764.

Fischer E (1916) Versuch über die Vererbung der Empfänglichkeit von Pflanzen für parasitische Pilze. Verhandlungen der Schweizerischen Naturforschenden Gesellschaft 98(II): 164–165.

Fischer MA, Adler W, Oswald K (2008) Exkursionsflora für Österreich, Liechtenstein und Südtirol. 3., verbesserte Auflage. Oberösterreichische Landesmuseen. Linz, 1392 pp.

Frey P, Gérard P, Feau N, Husson C, Pinon J (2005) Variability and population biology of *Melampsora* rusts on poplars. In: Pei MH, McCracken AR (Eds) Rust diseases of willow and poplar. CABI Publishing, Wallingford [UK], Cambridge MA, 63–72. https://doi.org/10.1079/9780851999999.0063

Friesen N (1996) A taxonomic and chorological revision of the genus *Allium* L. sect *Schoenoprasum* Dumort. Candollea. 51: 461–473.

Fromme FD (1914) The morphology and cytology of the aecidium cup. The Botanical Gazette 58: 1–35. https://doi.org/10.1086/331372

Garibaldi A, Gilardi G, Ortu G, Gullino ML (2012) First Report of Rust Caused by *Pucciniastrum circaeae* on *Fuchsia* × *hybrida* in Italy. Plant Disease 96: 588. https://doi.org/10.1094/PDIS-11-11-0976-PDN

Gäumann E (1959) Die Rostpilze Mitteleuropas mit besonderer Berücksichtigung der Schweiz. Beiträge zur Kryptogamenflora der Schweiz 12, 1407 pp. Büchler & Co., Bern.

Gäumann E (1964) Die Pilze. Grundzüge ihrer Entwicklungsgeschichte und Morphologie. Zweite, umgearbeitete und erweiterte Auflage. Birkhäuser Verlag, Basel und Stuttgart, 541 pp.

Gjærum HB (1974) Nordens Rustsopper. Fungiflora, Oslo, 321 pp.

Gjærum HB, Cummins GB (1982) Rust fungi (Uredinales) on East African *Alchemilla*. Mycotaxon 15: 420–424.

Gjærum HB, Talgø V, Toppe B, Herrero ML, Stensvand A (2007) First Report of *Melampsora euphorbiae* on Poinsettia (*Euphorbia pulcherrima*) in Norway. Plant Health Progress 8. https://doi.org/10.1094/PHP-2007-0423-01-BR

Gold RE, Littlefield LJ (1979) Light and electron microscopy of the telial, pycnial, and aecial stages of *Melampsora lini*. Canadian Journal of Botany 57: 629–638. https://doi.org/10.1139/b79-081

Grill D, Pfeifhofer W, Esterbauer H (1984) Carotenoids in *Chrysomyxa* abietis infected spruce needles. European Journal of Forest Pathology 14: 296–301. https://doi.org/10.1111/j.1439-0329.1984.tb00176.x

Guyot AL (1938) Les Urédinées (ou Rouilles des Végétaux). Tome I. Genre *Uromyces*. a) Espèces parasites des plantes appartenant aux familles des Graminées, Cypéracées, Joncacées, Renonculacées, Polygonacées, Ombellifères, Campanulacées. Encyclopédie Mycologique VIII, 438 pp. Paul Lechevalier, Paris.

Guyot AL (1951) Les Urédinées (ou Rouilles des Végétaux). Tome II. Genre *Uromyces*. b) Espèces parasites des plantes appartenant aux familles des Liliacées, Amaryllidacées, Iridacées, Chénopodiacées, Plombaginées, Composées, Rosacées, Géraniacées, Primulacées, Scrophulariacées, Valérianacées. Encyclopédie Mycologique XV, 331 pp. Paul Lechevalier, Paris.

Guyot AL (1957) Les Urédinées (ou Rouilles des Végétaux). Tome III. Genre *Uromyces*. c) Espèces parasites des plantes appartenant à la

famille des Légumineuses. Encyclopédie Mycologique XXIX, 647 pp. Éditions Paul Lechevalier, Paris.

Guyot AL, Massenot M (1958) Contribution à l'étude des Urédinées du Sud-Est de la France. Uredineana 5(= Encyclopédie Mycologique XXXI): 461–505.

Haack O (1914) Der Kienzopf (*Peridermium pini* [Willd.] Kleb.). Seine Übertragung von Kiefer zu Kiefer ohne Zwischenwirt. Zeitschrift für das Forst- und Jagdwesen 46: 3–46.

Hafellner J, Grill D (1982) REM-Untersuchungen an *Milesia vogesiaca* und *Milesia whitei* (Uredinales). Plant Systematics and Evolution 141: 23–29. https://doi.org/10.1007/BF01006476

Hantula J, Kasanen R, Kaitera J, Moricca S (2002) Analyses of genetic variation suggest that pine rusts *Cronartium flaccidum* and *Peridermium pini* belong to the same species. Mycological Research 106: 203–209. https://doi.org/10.1017/S0953756201005457

Hantula J, Kurkela T, Hendry S, Yamaguchi T (2009) Morphological measurements and ITS sequences show that the new alder rust in Europe is conspecific to *Melampsoridium hiratsukanum* in East Asia. Mycologia 101: 622–631. https://doi.org/10.3852/07-164

Hardtke HJ, Dämmrich F, Klenke F, Rödel T (2021) Pilze in Sachsen. Band 1 und 2. Landesamt für Umwelt, Landwirtschaft und Geologie, Dresden, 1720 pp.

Helfer S (1992) The rust diseases of willows in Britain. Proceedings of the Royal Society of Edinburgh 98B: 119–134. https://doi.org/10.1017/S0269727000007491

Helfer S (2005) Overview of the rust fungi (Uredinales) occurring on Rosaceae in Europe. Nova Hedwigia 81: 325–370. https://doi.org/10.1127/0029-5035/2005/0081-0325

Helfer S (2013) *Coleosporium* in Europe. Mycotaxon 124: 87–99. https://doi.org/10.5248/124.87

Helfer S, Berndt R, Denchev CM, Moricca S, Scheuer C, Scholler M, St. Quinton JM (2011) A call for renewed and pan-European strategic effort on the taxonomy of rust fungi (Uredinales). Mycologica Balcanica 8: 79–81.

Henderson DM (1953) Some Scottish mountain rust fungi. Transactions of the British Mycological Society 36: 315–319. https://doi.org/10.1016/S0007-1536(53)80026-4

Henderson DM (1957) The *Melampsora epitea* complex on mountain willows in Scotland. Notes from the Royal Botanic Garden Edinburgh 22: 201–206.

Henderson DM (1969) Studies in the morphology of fungal spores I: The teliospores of *Puccinia prostii* and *Nyssopsora echinata*. Notes from the Royal Botanic Garden Edinburgh 29: 373–375.

Henderson DM (1973) Studies in the morphology of fungal spores: *Trachyspora intrusa*. Reports of the Tottori Mycological Institute 10: 163–168.

Henderson DM (2004) The rust fungi of the British Isles: a guide to identification by their host plants, with an appendix correcting and updating the 2000 checklist. Kew, 35 pp.

Henderson DM, Bennell AP (1979) British rust fungi: Additions and corrections. Notes from the Royal Botanic Garden Edinburgh 37: 475–502.

Henderson DM, Prentice HT (1977) The morphology of fungal spores: *Milesia blechni*. Notes from the Royal Botanic Garden Edinburgh 35: 415–417.

Hennen JF, Hennen MMW (2000) Terminology applied to sori and life cycles of rust fungi (Uredinales) from 1729 to 2000. Biológico (São Paulo) 62: 113–126.

Hiratsuka N (1936) A monograph of the Pucciniastreae. Memoirs of the Tottori Agricultural College 4. Published by the College, Tottori, 374 pp.

Hiratsuka N, Kaneko S (1975) Surface structure of *Coleosporium* spores. Reports of the Tottori Mycological Institute 12: 1–13.

Hiratsuka N, Sato S, Katsuya K, Kakishima M, Hiratsuka Y, Kaneko S, Ono Y, Sato T, Harada Y, Hiratsuka T, Nakayama K (1992) The rust flora of Japan. Tsukuba Shuppankai, Tsukuba, Ibaraki, Japan, 1205 pp.

Hiratsuka Y (1968) Morphology and cytology of aeciospores and aeciospore germ tubes of host-alternating and pine-to-pine races of *Cronartium flaccidum* in northern Europe. Canadian Journal of Botany 46: 1119–1122. https://doi.org/10.1139/b68-147

Hiratsuka Y (1969) Endocronartium, a new genus for autoecious pine stem rusts. Canadian Journal of Botany 47: 1493–1495. https://doi.org/10.1139/b69-212

Hiratsuka Y (1971) Spore surface morphology of pine stem rusts of Canada as observed under a scanning electron microscope. Canadian Journal of Botany 49: 371–372. https://doi.org/10.1139/b71-061

Hiratsuka Y (1973a) Sorus development, spore morphology, and nuclear condition of *Gymnosporangium gaeumannii* ssp. *albertense*. Mycologia 65: 137–144. https://doi.org/10.1080/00275514.1973.12019412

Hiratsuka Y (1973b) The nuclear cycle and the terminology of spore states in Uredinales. Mycologia 65: 432–443. https://doi.org/10.1080/00275514.1973.12019451

Hiratsuka Y (1975) Recent controversies on the terminology of rust fungi. Reports of the Tottori Mycological Institute 12: 99–104.

Hiratsuka Y (1995) Pine stem rusts of the world – frame work for a monograph. In: Kaneko S, Katsuya K, Kakishima M, Ono Y (Eds) Proceedings of the Fourth Conference of the IUFRO Rusts of Pines Working Party. Tsukuba, 1–9.

Hiratsuka Y, Cummins GB (1963) Morphology of the spermogonia of the rust fungi. Mycologia 55: 487–507. https://doi.org/10.1080/00275514.1963.12018040

Hiratsuka Y, Sato S (1982) Morphology and Taxonomy of Rust Fungi. In: Scott KJ, Chakravorty AK (Eds) The Rust Fungi. Academic Press, London-New York, 1–36.

Hiratsuka Y, Morf W, Powell JM (1966) Cytology of the aeciospores and aeciospore germ tubes of *Peridermium* harknessiii and *P. stalactiforme* of the *Cronartium coleosporioides* complex. Canadian Journal of Botany 44: 1639–1643. https://doi.org/10.1139/b66-175

Hoch PC, Lievens AW, Raven PH, Jarvis CE (1995) (1159) Proposal to reject the name *Epilobium alpinum* L. (Onagracae). Taxon 44: 237–239. https://doi.org/10.2307/1222453

Hofsten A von, Holm L (1968) Studies on the fine structure of aeciospores. I. Grana Palynologica 8: 235–251. https://doi.org/10.1080/00173136809427469

Holm L (1964) Études Urédinologiques. 2. Les écidies sur *Ranunculus Ficaria*. Svensk Botanik Tidskrift 58: 105–112.

Holm L (1967) Études Urédinologiques. 5–7. Svensk Botanik Tidskrift 61: 231–251.

Holm L (1968) Études Urédinologiques. 8. *Gymnosporangium gaeumanni* – une espèce primitive? Svensk Botanik Tidskrift 62: 463–466.

Holm L (1973) Some notes on rust terminology. Reports of the Tottori Mycological Institute 10: 183–187.

Holm L (1984) Terminology of life cycle in rust fungi. Reports of the Tottori Mycological Institute 22: 221–225.

Holm L (1987) The terminology of rusts: Suggestions for a compromise. Notes from the Royal Botanic Garden Edinburgh 44: 433–435.

Holm L, Dunbar A, Hofsten A von (1970) Studies on the fine structure of aeciospores II. Svensk Botanik Tidskrift 64: 380–387.

Huber JA, Poeverlein H (1954) Die Uredineen (Rostpilze) Schwabens. (Fortsetzung). Abhandlungen des Naturwissenschaftlichen Vereins für Schwaben e.V. in Augsburg 10: 51–96.

Hurtado S, Ramstedt M (2002) AFLP comparison of distant *Melampsora epitea* (willow rust) populations. Mycological Research 106: 1400–1407. https://doi.org/10.1017/S0953756202006846

Hylander N, Jørstad I, Nannfeldt JA (1953) Enumeratio Uredinearum Scandinavicarum. Opera Botanica 1(1). Almqvist & Wiksell, Stockholm, 102 pp.

ICN [Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen, PS, Knapp S, Marhold K, Prado J, Prud'homme Van Reine WF, Smith GF, Wiersema JH, Turland NJ (Eds)] (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). Regnum Vegetabile 154. Koeltz Scientific Books, Königstein, Germany, [XXX +] 208 pp.

ICN [Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber WH, Li DZ, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (Eds)] (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten, [XXXVIII +] 254 pp. https://doi.org/10.12705/Code.2018

Index Fungorum (2024) [updated continuously] Royal Botanic Gardens, Kew, Landcare Research New Zealand, Institute of Microbiology, Chinese Academy of Science. https://www.indexfungorum.org [accessed January 2024]

Jaap O (1915) Sechstes Verzeichnis zu meinem Exsiccatenwerk „Fungi selecti exsiccati", Serien XXI–XXIV (Nummern 501–600), nebst Beschreibungen neuer Arten und Bemerkungen. Verhandlungen des Botanischen Vereins für die Provinz Brandenburg 56[1914]: 77–92.

Jacky E (1899) Untersuchungen über einige schweizerische Rostpilze. Berichte der Schweizerischen Botanischen Gesellschaft 9: 49–78.

Jage H, Scholler M, Klenke F (2010) Phytoparasitische Kleinpilze aus dem bayerischen und baden-württembergischen Allgäu. andrias (Karlsruhe) 18: 149–192[, 8 Tafeln].

Janchen E (1957) Catalogus Florae Austriae. Ein systematisches Verzeichnis der auf österreichischem Gebiet festgestellten Pflanzenarten. I. Teil: Pteridophyten und Anthophyten. Heft 2 (Dialypetalae). Österreichische Akademie der Wissenschaften, Wien, 177–440.

Janchen E (1958) Catalogus Florae Austriae. Ein systematisches Verzeichnis der auf österreichischem Gebiet festgestellten Pflanzenarten. I. Teil: Pteridophyten und Anthophyten. Heft 1 – 4. Österreichische Akademie der Wissenschaften, Wien, 441–710.

Jørstad I (1940) Uredinales of Northern Norway. Skrifter udgitt av Det Norske Videnskaps-Akademi i Oslo, Matematisk-Naturvidenskapelig Klasse (1940), 6: 1–145.

Jørstad I (1951) The Uredinales of Iceland. Skrifter udgitt av Det Norske Videnskaps-Akademi i Oslo, I. Matematisk-Naturvidenskapelig Klasse, Nr. 2: 1–87.

Joerstad [Jørstad] I (1953) Pucciniastreae and Melampsoreae of Norway. Uredineana 4(= Encyclopédie Mycologique XXIV): 91–123.

Jörstad [Jørstad] I (1960) The Norwegian rust species arranged alphabetically after host families and host genera, with short descriptions, mainly of macroscopical characters. Nytt Magasin for Botanikk 8: 103–146.

Jørstad I (1964a) Observations on life-cycles, spore-forms and alpine occurrence of the Norwegian Uredinales. Nytt Magasin for Botanikk 11: 27–45.

Jörstad [Jørstad] I (1964b) The distribution within Norway of rust fungi (Uredinales) compared with the distribution of their hosts. Nytt Magasin for Botanikk 11: 109–141.

Jørstad I, Nannfeldt JA (1958) Additions and corrections to "Enumeratio Uredinearum Scandinavicarum". Botaniska Notiser 111: 306–318.

Kaitera J, Seitamäki L, Hantula J, Jalkanen R, Kurkela T (1999) Morphological variation of *Peridermium pini* and *Cronartium flaccidum* aeciospores. Mycological Research 103: 677–683. https://doi.org/10.1017/S0953756298007503

Kaneko S (1981) The species of *Coleosporium*, the causes of pine needle rusts, in the Japanese Archipelago. Reports of the Tottori Mycological Institute 19: 1–159.

Kaneko S, Hiratsuka N (1982) Taxonomic significance of the urediniospore germpores in the pucciniastraceous and melampsoraceous rust fungi. Transactions of the Mycological Society of Japan 23: 201–210.

Kaneko S, Hiratsuka N (1983) A new species of *Melampsoridium* on *Carpinus* and *Ostrya*. Mycotaxon 18: 1–4.

Kaneko S, Kakishima M, Ono Y (1990) *Coleosporium* (Uredinales) from Nepal. In: Watanabe M, Malla SB (Eds) Cryptogams of the Himalayas. Vol. 2. Central and Eastern Nepal. National Science Museum, Tsukuba, Japan, 85–90.

Kern FD (1973a) A revised taxonomic account of *Gymnosporangium*. Pennsylvania State University Press, London, [IX +] 134 pp.

Kern FD (1973b) A host survey of *Gymnosporangium*. Mycopathologia et Mycologia Applicata 51: 99–101. https://doi.org/10.1007/BF02141290

Kirk PM, Cannon PF, Minter DW, Stalpers JA [Eds] (2008) Ainsworth and Bisby's Dictionary of the Fungi. 10th edition. CAB International, 771 pp. https://doi.org/10.1079/9780851998268.0000

Klebahn H (1890a) Neue Untersuchungen und Beobachtungen über die Blasenroste der Kiefern. Hedwigia 29: 27–35.

Klebahn H (1890b) Erster Beitrag zur Schmarotzerpilz-Flora Bremens. Abhandlungen herausgegeben vom Naturwissenschaftlichen Verein zu Bremen 11: 325–343.

Klebahn H (1900) Kulturversuche mit Rostpilzen. VIII. Jahrbücher für wissenschaftliche Botanik 34: 347–404.

Klebahn H (1904) Die wirtswechselnden Rostpilze. Versuch einer Gesamtdarstellung ihrer biologischen Verhältnisse. Borntraeger, Berlin, 447 pp. https://doi.org/10.5962/bhl.title.29948

Klebahn H (1908) Kulturversuche mit Rostpilzen XIII. Zeitschrift für Pflanzenkrankheiten 17(1907): 129–157.

Klebahn H (1912) Kulturversuche mit Rostpilzen XIV. Zeitschrift für Pflanzenkrankheiten 22: 321–350.

Klebahn H (1914) [published in five fascicles 1912, 1913, 1913, 1913, 1914] Uredineen. In: Kryptogamenflora der Mark Brandenburg, Band Va. Pilze III: 69–904, 925–946. Verlag von Gebrüder Borntraeger, Leipzig. [Numerous line drawings from this book are reproduced here with permission from the publishing house Borntraeger-J. Cramer, Stuttgart (https://www.borntraeger-cramer.de).]

Klebahn H (1938) Offene Fragen und neue Beobachtungen über die rindenbewohnenden Blasenroste der Kiefern, nebst Bemerkungen über einige andere Rostpilze. Zeitschrift für Pflanzenkrankheiten (Pflanzenpathologie) und Pflanzenschutz 48: 369–410.

Klenke F, Scholler M (2015) Pflanzenparasitische Kleinpilze. Bestimmungsbuch für Brand-, Rost-, Mehltau-, Flagellatenpilze und

Wucherlingsverwandte in Deutschland, Österreich, der Schweiz und Südtirol. Springer Verlag, Berlin, Heidelberg, [XV +] 1172 pp. https://doi.org/10.1007/978-3-662-46162-4

Kruse J (2024) [updated continuously] (Obligat) Phytoparasitische Kleinpilze. Mitteleuropa mit Schwerpunkt Deutschland. https://www.phytoparasiten.de [retrieved February 2024]

Kruse J, Kummer V, Thiel H (2014) Bemerkenswerte Funde phytoparasitischer Kleinpilze (3). Zeitschrift für Mykologie 80: 593–626.

Kuprevič VF, Uljaniščev VI (1975) Opredelitel ržavčinnych gribov SSSR [Determination key of rust fungi of the USSR]. Cast I. Sem. Melampsoraceae i nekotorye rody sem. Pucciniaceae. Izdatelstvo "Nauka i Technika", Minsk, 334 pp.

Kurkela T, Hanso M, Hantula J (1999) Differentiating characters between *Melampsoridium* rusts infecting birch and alder leaves. Mycologia 91: 987–992. https://doi.org/10.1080/00275514.1999.12061108

Kursanov L (1922) Recherches morphologiques et cytologiques sur les Urédinées. Bulletin de la Société des Naturalistes de Moscou, Section Biologique, nouvelle série, 31[1917]: 1–129.

Laundon GF (1965a) The generic names of Uredinales. Mycological Papers 99: 1–24.

Laundon GF (1965b) Rust Fungi III: on Alangiaceae, Amaranthaceae and Amaryllidaceae. Mycological Papers 102: 1–52.

Laundon GF (1967) Terminology in the rust fungi. Transactions of the British Mycological Society 50: 189–194. https://doi.org/10.1016/S0007-1536(67)80029-9

Laundon GF (1972) Delimitation of aecial from uredinial states. Transactions of the British Mycological Society 58: 344–346. https://doi.org/10.1016/S0007-1536(72)80168-2

Laundon GF (1973) Uredinales. In: Ainsworth GC, Sparrow FK, Sussman AS (Eds) The Fungi. An Advanced Treatise. Vol. IV B. A Taxonomic Review with Keys: Basidiomycetes and Lower Fungi. Academic Press, New York-London, 247–279.

Laundon GF (1975) Taxonomy and nomenclature notes on Uredinales. Mycotaxon 3: 133–161.

Laundon GF (1976) *Peridermium* (Fungi). Taxon 25: 186–187. https://doi.org/10.2307/1220441

Laundon GF, Holm L (1976) Nomenclature of *Melampsoridium betulinum*. Mycotaxon 4: 296–298.

Lee SK, Kakishima M (1999) Aeciospore surface structures of *Gymnosporangium* and *Roestelia* (Uredinales). Mycoscience 40: 109–120. https://doi.org/10.1007/BF02464289

Leppik EE (1973) Origin and evolution of conifer rusts in the light of continental drift. Mycopathologia et Mycologia Applicata 49: 121–136. https://doi.org/10.1007/BF02050854

Liang YM (2006) Taxonomic evaluation of morphologically similar species of *Pucciniastrum* in Japan based on comparative analyses of molecular phylogeny and morphology. Diss. Univ. Tsukuba, 103[+40] pp.

Liang YM, Tian CM, Kakishima M (2006) Phylogenetic relationships on 14 morphologically similar species of *Pucciniastrum* in Japan based on rDNA sequence data. Mycoscience 47: 137–144. https://doi.org/10.1007/S10267-006-0284-X

Lindfors T (1913) Aufzeichnungen über parasitische Pilze in Lule Lappmark. Svensk Botanisk Tidskrift 7: 39–57.

Littlefield LJ, Heath MC (1979) Ultrastructure of Rust Fungi. Academic Press, New York, San Francisco, London, [XI +] 277 pp. https://doi.org/10.1016/B978-0-12-452650-1.50012-4

Littlefield LJ, Schimming WK (1989) Size and shape of urediniospores as influenced by ambient relative humidity. Mycotaxon 36: 187–204.

Lohsomboon P, Kakishima M, Ono Y (1990a) A revision of the genus *Nyssopsora*. Mycological Research 94: 907–922. https://doi.org/10.1016/S0953-7562(09)81305-1

Lohsomboon P, Kakishima M, Ono Y (1990b) A revision of the genus *Triphragmium*. Transactions of the Mycological Society of Japan 31: 215–226.

Lohsomboon P, Kakishima M, Ono Y (1990c) The genus *Triphragmiopsis*. Transactions of the Mycological Society of Japan 31: 335–343.

Longo N, Moriondo F, Naldini B (1970) Biologia ed epidemiologia di *Melampsora pinitorqua* Rostr. Annali, Accademia Italiana di Scienze Forestali 19: 83–175.

Longo N, Moriondo F, Naldini Longo B (1975) The status of *Melampsora pinitorqua* Rostr. in Italy. European Journal of Forest Pathology 5: 147–152. https://doi.org/10.1111/j.1439-0329.1975.tb00459.x

Longo N, Moriondo F, Naldini Longo B (1979) Ultrastructural observations on teliospores of *Melampsora pinitorqua* Rostr. Caryologia 32: 223–240. https://doi.org/10.1080/00087114.1979.10796789

Longo N, Naldini B, Paolillo A, Drovandi F, Gonnelli T (2002) Signs of resistance to *Melampsora larici-tremulae* on species of *Pinus* hosts of *Melampsora pinitorqua*: implications regarding the taxonomic relationship between the two rust fungi. Phytopathologia Mediterranea 41: 212–219.

López-Franco RM, Hennen JF (1990) The genus *Tranzschelia* (Uredinales) in the Americas. Systematic Botany 15: 560–591. https://doi.org/10.2307/2419155

Magnus P (1905) Die Pilze (Fungi) von Tirol, Vorarlberg und Liechtenstein. In: Dalla Torre KW v., Sarntheim L v. (Eds) Flora der gefürsteten Grafschaft Tirol, des Landes Vorarlberg und des Fürstenthumes Liechtenstein, III. Band. Verlag der Wagner'schen Universitätsbuchhandlung, Innsbruck, [LIV +] 716 pp. https://doi.org/10.5962/bhl.title.3876

Magnus P (1909) Bemerkungen über einige Gattungen der Melampsoreen. Berichte der Deutschen Botanischen Gesellschaft 27: 320–327. https://doi.org/10.1111/j.1438-8677.1909.tb06805.x

Maier W, Begerow D, Weiss M, Oberwinkler F (2003) Phylogeny of the rust fungi: an approach using nuclear large subunit ribosomal DNA sequences. Canadian Journal of Botany 81: 12–23. https://doi.org/10.1139/b02-113

Maier W, Wingfield BD, Mennicken M, Wingfield MJ (2007) Polyphyly and two emerging lineages in the rust genera *Puccinia* and *Uromyces*. Mycological Research 111: 176–185. https://doi.org/10.1016/j.mycres.2006.11.005

Mains EB (1939) New and unusual species of Uredinales. Bulletin of the Torrey Botanical Club 66: 617–621. https://doi.org/10.2307/2480804

Maire R (1907) Contributions à l'étude de la flore mycologique des Pyrénées. Champignons récoltés à la session de la Société Botanique de France à Gavarnie et Cautarets en 1907. Bulletin de la Société Botanique de France 54: CXLIV–CLXV. https://doi.org/10.1080/00378941.1907.10831321

Majewski T (1977) Flora Polska. Grzyby (Mycota). Tom IX. Podstawczaki (Basidiomycetes), Rdzawnikowe (Uredinales) I. Państwowe Wydanictwo Naukowe, Warszawa–Kraków, 394 pp.

Majewski T (1979) Flora Polska. Grzyby (Mycota). Tom XI. Podstawczaki (Basidiomycetes). Rdzawnikowe (Uredinales) II. Państwowe Wydanictwo Naukowe, Warszawa–Kraków, 463 pp.

Maurer W (1996) Flora der Steiermark. Band I. Farnpflanzen (Pteridophyten) und freikronblättrige Blütenpflanzen (Apetale und Dialypetale). IHW-Verlag, Eching, 311 pp.

Mayor E (1924) Notes mycologiques [V]. Bulletin de la Société Neuchâteloise des Sciences Naturelles 48(1923): 367–396.

Mayor E (1927) Notes mycologiques VI. Bulletin de la Société Neuchâteloise des Sciences Naturelles 51(1926): 53–76.

Mayor E (1958) Catalogue des Péronosporales, Taphrinales, Erysiphacées, Ustilaginales et Urédinales du canton de Neuchâtel. Mémoires de la Société Neuchâteloise des Sciences Naturelles 9(1), 202 pp.

Mayor E (1960) Excursions dans les Alpes-Maritimes. Bulletin de la Société mycologique de France 76: 291–301.

Mayor E (1969) Recherches mycologiques dans le Queyras. Bulletin de la Société Mycologique de France 85: 159–193.

Mayor E (1970) Micromycètes récoltés dans les Pyrénées. Bulletin de la Société Botanique Suisse 80: 252–268.

Mayor E (1971) Notes mycologiques suisses III. Bulletin de la Société Botanique Suisse 81: 19–26.

Mayor E (1972) Micromycètes observés dans les jardins de l'Institut de botanique de Neuchâtel. Bulletin de la Société Neuchâteloise des Sciences Naturelles 95: 81–88.

McCain JW, Hennen JF (1990) Taxonomic notes on *Frommeëlla* (Uredinales) - 1. Mycotaxon 39: 249–256.

McNabb RFR, Laurenson JB (1965) A rust of cultivated Fuchsias. New Zealand Journal of Agricultural Research 8: 336–339. https://doi.org/10.1080/00288233.1965.10422364

Melekhov IS (1946) O povrezhdeniĭakh elovykh lesov severnoĭ taĭgi rzhavchinnym gribom *Chrysomyxa ledi* [On the damage to the fir forests of the northern taiga by the rust fungus *Chrysomyxa ledi*]. Arkhangel'sk Lesotekh. Inst. im. V. V. Kuibysheva, Sborn. Nauch.-Issled. Rabot. 8: 59–75. [in Russian]

Migula W (1917) Die Brand- u. Rostpilze. Ein Hilfsbuch zu ihrem Erkennen, Bestimmen, Sammeln, Untersuchen und Präparieren. Franckh'sche Verlagshandlung, Stuttgart, 132 pp.[, 10 Tafeln.]

Minkevičius A (1937) Grundzüge der Uredineen-Flora Litauens. Mémoires de la Faculté des Sciences de l'Université 'Vytautas le Grand' (Kaunas) 11: 335–450. [in Lithuanian, with summary in German]

Moesz G von (1941) Fungi Hungariae. IV. Basidiomycetes - Pars 1. Uredineae. Annales Historico-Naturales Musei Nationalis Hungarici 34: 72–158.

Moricca S, Benigno A, Oliveira Longa CM, Cacciola SO, Maresi G (2021) First Documentation of Life Cycle Completion of the Alien Rust Pathogen *Melampsoridium hiratsukanum* in the Eastern Alps Proves Its Successful Establishment in This Mountain Range. Journal of Fungi 7: 617. [18 pp.] https://doi.org/10.3390/jof7080617

Müller J (2003) Rost-, Brand- und Falsche Mehltaupilze neu für Mähren und tschechisch Schlesien. Czech Mycology 55: 277–290. https://doi.org/10.33585/cmy.55313

Müller [Mueller] W (1907) Zur Kenntnis der *Euphorbia* bewohnenden Melampsoren. Centralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, Zweite Abteilung 19: 441–460, 544–563.

MycoBank (2024) [updated continuously] Fungal Databases, Nomenclature & Species Banks. https://www.mycobank.org/ [accessed January 2024]

Naldini B, Longo N, Drovandi F, Gonnelli T, Moriondo F (1992) Observations on some Italian provenances of *Melampsora populnea*. III. Presence of *Melampsora pinitorqua* in possible outbreak areas. European Journal of Forest Pathology 22: 188–191. https://doi.org/10.1111/j.1439-0329.1992.tb01446.x

Naldini Longo B, Longo N, Moriondo F, Drovandi F (1985) Observations on some Italian provenances of *Melampsora populnea*. I. Studies for identification of *Melampsora pinitorqua* and *M. larici-tremulae*. European Journal of Forest Pathology 15: 432–444. https://doi.org/10.1111/j.1439-0329.1985.tb00900.x

Obermayer W (2024) [updated continuously] Plants of Styria. University of Graz, Austria. https://homepage.uni-graz.at/de/walter.obermayer/plants-of-styria.uni-graz.at [accessed January 2024]

Œrsted AS (1865) Vorläufige Berichterstattung über einige Beobachtungen, welche beweisen, daß *Podisoma sabinae* und *Roestelia cancellata* wechselnde Erzeugnisse derselben Pilzart sind. Botanische Zeitung (Berlin) 23: 291–293.

Ono Y (1980) Is *Uredo iyoensis* dimorphic? Mycologia 72: 1195–1199. https://doi.org/10.1080/00275514.1980.12021301

Ono Y (1994) *Tranzschelia asiatica* sp. nov. and its taxonomic relationship to *Tranzschelia arthurii*. Canadian Journal of Botany 72: 1178–1186. https://doi.org/10.1139/b94-144

Ono Y (2006) Taxonomic implications of life cycle and basidium morphology of *Ochropsora ariae* and *O. nambuana* (Uredinales). Mycoscience 47: 145–151. https://doi.org/10.1007/S10267-006-0285-9

Ono Y, Buriticá P, Hennen JF (1992) Delimitation of *Phakopsora*, *Physopella* and *Cerotelium* and their species on Leguminosae. Mycological Research 96: 825–850. https://doi.org/10.1016/S0953-7562(09)81029-0

Padamsee M, McKenzie EHC (2014) A new species of rust fungus on the New Zealand endemic plant, *Myosotidium*, from the isolated Chatham Islands. Phytotaxa 174: 223–230. https://doi.org/10.11646/phytotaxa.174.4.3

Parmelee JA (1989) The rusts (Uredinales) of arctic Canada. Canadian Journal of Botany 67: 3315–3365. https://doi.org/10.1139/b89-407

Peace TR (1962) Pathology of trees and shrubs with special reference to Britain. Clarendon Press, Oxford, [XX +] 723 pp.[, 16 plates.]

Pei MH (2005) A Brief Review of *Melampsora* Rusts on Salix. In: Pei MH, McCracken AR (Eds) Rust diseases of willow and poplar. CABI Publishing, Wallingford [UK], Cambridge MA, 11–28. https://doi.org/10.1079/9780851999999.0000

Pei MH, Ruiz C (2000) AFLP evidence of distinct patterns of life-cycle in two forms of *Melampsora* rust on *Salix viminalis*. Mycological Research 104: 937–942. https://doi.org/10.1017/S0953756200002574

Pei MH, Bayon C, Ruiz C (2005a) Phylogenetic position of *Melampsora* in rust fungi inferred from ribosomal DNA sequences. In: Pei MH, McCracken AR (Eds) Rust diseases of willow and poplar. CABI Publishing, Wallingford [UK], Cambridge MA, 1–9. https://doi.org/10.1079/9780851999999.0001

Pei MH, Bayon C, Ruiz C (2005b) Phylogenetic relationships in some *Melampsora* rusts on Salicaceae assessed using rDNA sequence information. Mycological Research 109: 401–409. https://doi.org/10.1017/S0953756205002479

Persoon CH (1801) Synopsis methodica fungorum, sistens enumerationem omnium huc usque detectarum specierum, cum brevibus descriptionibus nec non synonymis et observationibus selectis. [I, II]. H. Dieterich, Göttingen, [XXXII +] 708 pp. https://doi.org/10.5962/bhl.title.166151

Peterson RS (1967) The *Peridermium* species on pine stems. Bulletin of the Torrey Botanical Club 94: 511–542. https://doi.org/10.2307/2483569

Peterson RS, Oehrens E (1978) *Mikronegeria alba* (Uredinales). Mycologia 70: 321–331. https://doi.org/10.1080/00275514.1978.12020232

Petrova RD, Denchev CM (2004) A taxonomic study of Phragmidiaceae (Uredinales) in Bulgaria. Mycologia Balcanica 1: 95–115.

Pfunder M, Roy BA (2000) Pollinator-mediated interactions between a pathogenic fungus, *Uromyces pisi* (Pucciniaceae), and its host plant, *Euphorbia cyparissias* (Euphorbiaceae). American Journal of Botany 87: 48–55. https://doi.org/10.2307/2656684

Pfunder M, Schürch S, Roy B (2001) Sequence variation and geographic distribution of pseudoflower-forming rust fungi (*Uromyces pisi* s. lat.) on *Euphorbia cyparissias*. Mycological Research 105: 57–66. https://doi.org/10.1017/S0953756200003208

Phillips DH, Burdekin DA (1982) Diseases of Forest and Ornamental Trees. The MacMillan Press Ltd., London and Basingstoke, [XVI +] 435 pp. https://doi.org/10.1007/978-1-349-06177-8

Pinon J (1973) Les rouilles du peuplier en France. Systematique et repartition du stade uredien. European Journal of Forest Pathology 3: 221–228. https://doi.org/10.1111/j.1439-0329.1973.tb00398.x

Pinon J (1986) Situation of *Melampsora medusae* in Europe. EPPO Bulletin 16: 547–551. https://doi.org/10.1111/j.1365-2338.1986.tb00321.x

Pinon J, Frey P (1997) Structure of *Melampsora larici-populina* populations on wild and cultivated poplar. European Journal of Plant Pathology 103: 159–173. https://doi.org/10.1023/A:1008650128568

Poelt J (1984) *Milesia exigua* – ein für Mitteleuropa neuer Rostpilz in der Steiermark. Sydowia 36: 252–254.

Poelt J (1985) Catalogus Florae Austriae, Teil III, Heft 1, Uredinales. Österreichische Akademie der Wissenschaften, Wien, 192 pp.

Poelt J, Zwetko P (1991) Über einige bemerkenswerte Funde von entweder adventiven oder apophytischen Rostpilzen der Steiermark. Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark 121: 65–72.

Poelt J[†], Zwetko P (1997) Die Rostpilze Österreichs. 2., revidierte und erweiterte Auflage des Catalogus Florae Austriae, III. Teil, Heft 1, Uredinales. Biosystematics and Ecology Series 12, 365 pp. Österreichische Akademie der Wissenschaften, Wien.

Poeverlein H (1937) Die Verbreitung der süddeutschen Uredineen. Berichte der Bayerischen Botanischen Gesellschaft 22: 86–120.

POWO (2024) [updated continuously] Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. http://www.plantsoftheworldonline.org/ [retrieved January 2024]

Raabe A (1938) Parasitische Pilze aus der Umgebung von Tübingen. Ein Beitrag zur Kryptogamenflora Südwestdeutschlands. Hedwigia 78: 1–106.

Riegler-Hager H, Scheuer C, Zwetko P (2003) Der Erlen-Rost Melampsoridium hiratsukanum in Österreich. Wulfenia 10: 135–143.

Ritz CM, Maier WFA, Oberwinkler F, Wissemann V (2005) Different evolutionary histories of two *Phragmidium* species infecting the same dog rose hosts. Mycological Research 109: 603–609. https://doi.org/10.1017/S0953756205002844

Roll-Hansen F, Roll-Hansen H (1981) *Melampsoridium* on Alnus in Europe. *M. alni* conspecific with *M. betulinum*. European Journal of Forest Pathology 11: 77–87. https://doi.org/10.1111/j.1439-0329.1981.tb00073.x

Sakuma T (1992) Pathogenic races of *Gymnosporangium asiaticum* on Japanese pear and pathogenicity to some species in genus *Pyrus*. Bulletin of the Fruit Tree Research Station, No. 22: 67–78.

Samils B, Kaitera J, Persson T, Stenlid J, Barklund P (2021) Relationship and genetic structure among autoecious and heteroecious populations of *Cronartium pini* in northern Fennoscandia. Fungal Ecology 50: 101032. [10 pp.] https://doi.org/10.1016/j.funeco.2020.101032

Sato S, Katsuya K, Hiratsuka Y (1993) Morphology, taxonomy and nomenclature of *Tsuga*-Ericaceae rusts. Transactions of the Mycological Society of Japan 34: 47–62.

Sato T, Sato S (1980) The caeomoid uredinium of *Xenodochus carbonarius*. Transactions of the Mycological Society of Japan 21: 411–416.

Sato T, Sato S (1982) Aeciospore surface structure of the Uredinales. Transactions of the Mycological Society of Japan 23: 51–63.

Savile DBO (1950) North American species of *Chrysomyxa*. Canadian Journals of Research, C, 28: 318–330. https://doi.org/10.1139/cjr50c-018

Savile DBO (1955a) A phylogeny of the Basidiomycetes. Canadian Journal of Botany 33: 60–104. https://doi.org/10.1139/b55-006

Savile DBO (1955b) *Chrysomyxa* in North America – additions and corrections. Canadian Journal of Botany 33: 487–496. https://doi.org/10.1139/b55-039

Savile DBO (1968) The case against "uredium". Mycologia 60: 459–464. https://doi.org/10.1080/00275514.1968.12018593

Savile DBO (1973) Aeciospore types in *Puccinia* and *Uromyces* attacking Cyperaceae, Juncaceae and Poaceae. Reports of the Tottori Mycological Institute 10: 225–241.

Savile DBO (1974) *Phragmidium fusiforme* var. *novi-boreale*. Fungi Canadenses 54: 1–2.

Savile DBO (1976) Evolution of the Rust Fungi (Uredinales) as reflected by their ecological problems. Evolutionary Biology 9: 137–207. https://doi.org/10.1007/978-1-4615-6950-3_4

Savile DBO (1979) Fungi as aids in higher plant classification. The Botanical Review (Lancaster, New York) 45: 377–503. https://doi.org/10.1007/BF02860873

Savile DBO (1988) Terminology of spore states in Uredinales. Mycotaxon 33: 387–389.

Savile DBO (1989) Raveneliaceae revisited. Canadian Journal of Botany 67: 2983–2994. https://doi.org/10.1139/b89-382

Scheuer C (2003) Mycotheca Graecensis, Fasc. 13–18 (Nr. 241–360). Fritschiana (Graz) 37: 1–47.

Scheuer C (2004) Mycotheca Graecensis, Fasc. 19 & 20 (Nr. 361–400) und alphabetisches Gesamtverzeichnis. Fritschiana (Graz) 46: 1–24.

Scheuer C (2015) Mycotheca Graecensis, Fasc. 25 (Nos 481–500). Fritschiana (Graz) 79: 1–9.

Scheuer C (2018) Dupla Graecensia Fungorum (2018, Nos 451–500). Fritschiana (Graz) 88: 1–19.

Scholler M, Lutz M, Aime MC (2019) Repeated formation of correlated species in *Tranzschelia* (Pucciniales). Mycological Progress 18: 295–303. https://doi.org/10.1007/s11557-018-1417-2

Scholler M, Braun U, Buchheit R, Schulte T, Bubner B (2022) Studies on European rust fungi, Pucciniales: molecular phylogeny, taxonomy, and nomenclature of miscellaneous genera and species in Pucciniastraceae and Coleosporiaceae. Mycological Progress 21: 64. [25 pp.] https://doi.org/10.1007/s11557-022-01810-3

Schön M (2014) Rostpilze (Uredinales, Phragmidiaceae) auf Schwarzfrüchtigen Brombeeren (*Rubus* Subgenus *Rubus*) in Deutschland. Schlechtendalia 27: 21–35.

Schratt-Ehrendorfer L, Niklfeld H, Schröck C, Stöhr O [Eds] (2022) Rote Liste der Farn- und Blütenpflanzen Österreichs. Stapfia 114. Land Oberösterreich, Linz, 357 pp.

Schröter J (1885–1889) [published in six fascicles 1885, 1886, 1887, 1888, 1889, 1889] Die Pilze Schlesiens. Erste Hälfte. In: Cohn F (Ed.) Kryptogamen-Flora von Schlesien. Dritter Band. J. U. Kern's Verlag (Max Müller), Breslau, 814 pp. https://doi.org/10.5962/bhl.title.45927

Shain L (1988) Evidence for formae speciales in the poplar leaf rust fungus, *Melampsora medusae*. Mycologia 80: 729–732. https://doi.org/10.1080/00275514.1988.12025608

Shattock RC, Preece TF (2000) Tranzschel revisited: Modern studies of the relatedness of different rust fungi confirm his Law. Mycologist 14: 113–117. https://doi.org/10.1016/S0269-915X(00)80086-5

Siwecki R (1990) Ultrastructure of *Melampsora larici-populina*. Reports of the Tottori Mycological Institute 28: 95–108.

Smith IM, Dunez J, Lelliott RA, Phillips DH, Archer SA (1988) European Handbook of Plant Diseases. Blackwell Scientific Publications, Oxford, etc., [XIV +] 583 pp. https://doi.org/10.1002/9781444314199

Smith JA, Blanchette RA, Newcombe G (2004) Molecular and morphological characterization of the willow rust fungus, *Melampsora epitea*, from arctic and temperate hosts in North America. Mycologia 96: 1330–1338. https://doi.org/10.1080/15572536.2005.11832882

Speer EO (1971) Untersuchungen an einigen parasitischen Pilzen und ihren Wirtspflanzen. Sydowia 25: 1–34.

Steimel J, Chen W, Harrington TC (2005) Development and characterization of microsatellite markers for the poplar rust fungi *Melampsora medusae* and *Melampsora larici-populina*. Molecular Ecology Notes 5: 484–486. https://doi.org/10.1111/j.1471-8286.2005.00964.x

Sydow H (1942) Mycotheca Germanica Fasc. LXIX–LXXII (no. 3401–3600). Annales Mycologici 40: 193–218.

Sydow H, Sydow P (1903) Neue und kritische Uredineen I. Annales Mycologici 1: 324–334.

Sydow P, Sydow H (1904) Monographia Uredinearum. Volumen I: Genus *Puccinia*. Gebr. Borntraeger, Leipzig, [XXV +] 972 pp.

Sydow P, Sydow H (1915) Monographia Uredinearum. Volumen III. Pucciniaceae (excl. Puccinia et Uromyces) – Melampsoraceae – Zaghouaniaceae – Coleosporiaceae. Gebr. Borntraeger, Leipzig, 726 pp.

Sydow P, Sydow H (1924) Monographia Uredinearum. Volumen IV. Uredineae imperfectae. Gebr. Borntraeger, Leipzig, [IV +] 512 pp.

Szabó I (2002a) First report of *Melampsoridium hiratsukanum* on common alder in Hungary. New Disease Reports (British Society for Plant Pathology) 5: 11. https://doi.org/10.1046/j.1365-3059.2002.00776.x

Szabó I (2002b) First report of *Melampsoridium hiratsukanum* on common alder in Hungary. Plant Pathology 51: 804. https://doi.org/10.1046/j.1365-3059.2002.00776.x

Teppner H, Gjaerum [Gjærum] H, Brandenburger W (1977) Ein für Europa neuer Rostpilz, *Pucciniastrum brachybotrydis* (Uredinales), in Österreich gefunden. Sydowia 29: 281–284.

Termorshuizen AJ, Swertz CA (2011) Roesten van Nederland. Dutch Rust Fungi. Publisher: Aad Termorshuizen, 423 pp.

Thiel H, Klenke F, Kruse J, Kummer V, Schmidt M (2023) Rote Liste und Gesamtartenliste der phytoparasitischen Kleinpilze Deutschlands [Brandpilzverwandte (Exobasidiomycetes p.p., Ustilaginomycetes p.p.), Rostpilzverwandte (Kriegeriaceae p.p., Microbotryales, Pucciniales), Wurzelknöllchenpilze (Entorrhizaceae), Echte Mehltaupilze (Erysiphaceae), Falsche Mehltaue (Peronosporaceae p.p.) und Weißroste (Albuginaceae)]. Naturschutz und Biologische Vielfalt 170(5), 347 pp. https://doi.org/10.19213/972175

Thiers BM (2024) [updated continuously] Index Herbariorum. The New York Botanical Garden, Steere Herbarium. https://sweetgum.nybg.org/science/ih/

Thirumalachar MJ, Cummins GB (1948) Status of the Rust Genera *Allopuccinia*, *Leucotelium*, *Edythea*, and *Ypsilospora*. Mycologia 40: 417–422. https://doi.org/10.1080/00275514.1944.12017719

Tranzschel VA (1927) Rust fungi and their bearing on the systematics of vascular plants. In: Festschrift for I. P. Borodin. Leningrad, 282–291. [in Russian]

Tulasne LR (1854) Second mémoire sur les Urédinées et les Ustilaginées. Annales des Sciences Naturelles, Botanique, 4e sér., 2: 77–196[, planches 7–12].

Urban Z, Marková J (2009) Catalogue of rust fungi of the Czech and Slovak Republics. Charles University Prague, Karolinum Press, 365 pp.

Van der Merwe M, Walker J, Ericson L, Burdon JJ (2008) Coevolution with higher taxonomic host groups within the *Puccinia/Uromyces* rust lineage obscured by host jumps. Mycological Research 112: 1387–1408. https://doi.org/10.1016/j.mycres.2008.06.027

Viennot-Bourgin G (1949) Les champignons parasites des plantes cultivées. I, II. Masson & Cie, Paris, 1850 pp.

Viennot-Bourgin G (1956) Mildious, oidiums, caries, charbons, rouilles des plantes de France. I Texte, II Atlas. Encyclopédie Mycologique 26 (317 pp.), 27 (89 planches). Lechevalier, Paris.

Vleugel J (1908) Zur Kenntnis der auf der Gattung *Rubus* vorkommenden *Phragmidium*-Arten. Svensk Botanisk Tidskrift 2: 123–138.

Vogler DR, Bruns TD (1993) Use of Molecular Characters to Identify Holomorphs: An Example from the Rust Genus *Cronartium*. In: Reynolds DR, Taylor JW (Eds) The Fungal Holomorph: Mitotic, Meiotic and Pleomorphic Speciation in Fungal Systematics. Proceedings of an International Symposium, Newport, Oregon, 4–7 August 1992. CAB International, Wallingford, 237–245.

Vogler DR, Epstein L, Cobb FWJ (1997) Nuclear behavior and evolution of two populations of the western gall rust fungus. Mycological Research 101: 791–797. https://doi.org/10.1017/S0953756296003346

Voglmayr H, Krisai-Greilhuber I, Kirisits T (2020) First report of *Coleosporium montanum* on *Symphyotrichum* in Austria and Europe. New Disease Reports 42: 24. https://doi.org/10.5197/j.2044-0588.2020.042.024

Voglmayr H, Schertler A, Essl F, Krisai-Greilhuber I (2022) Alien and cryptogenic fungi and oomycetes in Austria: an annotated checklist (2nd edition). Biological Invasions 25: 27–38. https://doi.org/10.1007/s10530-022-02896-2

Wahyuno D, Kakishima M, Ono Y (2002) Aeciospore surface structures of *Phragmidium* species parasitic on roses. Mycoscience 43: 159–167. https://doi.org/10.1007/S102670200023

Wahyuno D, Susan D, Kakishima M (2012) Occurrence of a rust disease of *Fuchsia* caused by *Pucciniastrum epilobii* in Indonesia. Australasian Plant Disease Notes 7: 143–146. https://doi.org/10.1007/s13314-012-0070-x

Webster J, Weber RWS (2007) Introduction to Fungi. Third Edition. Cambridge University Press, Cambridge, UK, [XIX +] 841 pp.

WFO (2024) [updated continuously] World Flora Online. Published on the Internet. http://www.worldfloraonline.org [accessed January 2024]

White FB (1878) Note on the zoology and botany of Glen Tilt. The Scottish Naturalist 4[1877–1878]: 160–163.

Wilson M, Henderson DM (1966) The British Rust Fungi. Cambridge University Press, London, New York, Cambridge, 384 pp.

Wingfield BD, Ericson L, Szaro T, Burdon JJ (2004) Phylogenetic patterns in the Uredinales. Australasian Plant Pathology 33: 327–335. https://doi.org/10.1071/AP04020

Wołczańska A (1999) *Melampsoridium hiratsukanum* (Uredinales), a new species for Poland. Acta Mycologica 34: 345–347. https://doi.org/10.5586/am.1999.023

Yadav S, Singh G, Rajwar S, Verma SK, Gupta SK, Singh R, Kharwar RN, Kumar S (2023) Nyssopsoraceae, a new family of Pucciniales to accommodate *Nyssopsora* spp. Current Research in Environmental & Applied Mycology (Journal of Fungal Biology) 13(1): 523–549.

Yu ZD, Liang J, Cao ZM, Guo ZQ, Dan JY, Zhao GC (2009) Nuclear behavior in the life cycle of *Melampsora larici-populina* Kleb. Journal of Food, Agriculture and Environment 7: 791–794.

Yun HY, Minnis AM, Kim YH, Castlebury LA, Aime MC (2011) The rust genus *Frommeëlla* revisited: a later synonym of *Phragmidium* after all. Mycologia 103: 1451–1463. https://doi.org/10.3852/11-120

Ziller WG (1954) Studies of western tree rusts: I. A new cone rust on Sitka spruce. Canadian Journal of Botany 32: 432–439. https://doi.org/10.1139/b54-039

Ziller WG (1959) Studies of western tree rusts. IV. *Uredinopsis hashiokai* and *U. pteridis* causing perennial needle rust of fir. Canadian Journal of Botany 37: 93–107. https://doi.org/10.1139/b59-009

Zwetko P (1993) Rostpilze (Uredinales) auf *Carex* im Ostalpenraum. Ein neues Artenkonzept. Bibliotheca Mycologica 153. J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin-Stuttgart, 222 pp.

Zwetko P (2000) Die Rostpilze Österreichs. Supplement und Wirt-Parasit-Verzeichnis zur 2. Auflage des Catalogus Florae Austriae III. Teil, Heft 1, Uredinales. Biosystematics and Ecology Series 16. Österreichische Akademie der Wissenschaften, Wien, 67 pp.

Zwetko P, Blanz P (2004) Die Brandpilze Österreichs. Doassansiales, Entorrhizales, Entylomatales, Georgefischeriales, Microbotryales, Tilletiales, Urocystales, Ustilaginales. Catalogus Florae Austriae III/3. Biosystematics and Ecology Series 21. Österreichische Akademie der Wissenschaften, Wien, 240 pp.

Zwetko P, Blanz P (2012) Aeciospore types in rusts on *Ranunculus* and allied genera. In: Pfosser M, Blanz P (Red.) Pilze – Fungi [Ausstellung im Biologiezentrum der Oberösterreichischen Landesmuseen, 30. März 2012–4. November 2012]. Stapfia 96. Land Oberösterreich, Linz, 105–121.

Zwetko P[†], Blanz P (2018) Distinctiveness of aecia and aeciospores on conifers. In: Blanz P (Ed.) Biodiversity and Ecology of Fungi, Lichens, and Mosses. Kerner von Marilaun Workshop 2015 in memory of Josef Poelt. Biosystematics and Ecology Series 34. Verlag der Österreichischen Akademie der Wissenschaften, Wien, 271–287. https://doi.org/10.1553/0x003892e7

Zwetko P, Pfeifhofer HW (1991) Carotinuntersuchungen an Rostpilzsporen. Bedeutung für die Physiologie und Taxonomie. Nova Hedwigia 52: 251–266.

Appendix 1

Alphabetical host-parasite index

Table A1. Alphabetical host-parasite-index. All known host species from the area are compiled alphabetically, except for erratic introduced hosts of mediterranean rusts. Confirmed host-parasite combinations from Austria are given in ***bold italics***, those expected but not yet confirmed in *italics*. Names of collective species (e.g., *Melampsora euphorbiae* s.l., *Coleosporium tussilaginis* s.l.) or generic names (e.g., *Melampsora* sp., *Milesina* sp.) are only used if a more precise identification was not available. This applies especially for aecial stages of certain genera or species groups. Uncertain host identifications and host-parasite combinations are marked by '?', in line with the information given in the treatments of the rust species in the main chapter ('Rust taxa…'). A considerable number of host-parasite combinations, especially of conifer rusts and *Melampsora* species on *Salix* and *Populus*, are based on results of inoculation experiments (e.g., cited in Gäumann 1959).

Host taxon	Rust taxon	Sori and spores
Abies alba	***Calyptospora columnaris***	[0],I
	Hyalopsora aspidiotus	0,I
	Melampsora abietis-caprearum (*M. epitea* s.l.)	0,I
	Melampsorella elatina	0,I
	***Milesina* sp.**	0,I
	Milesina blechni	0,I
	Milesina carpatica	0,I
	Milesina exigua	0,I
	Milesina feurichii	0,I
	Milesina kriegeriana	0,I
	Milesina murariae	0,I
	Milesina polypodii	0,I
	Milesina scolopendrii	0,I
	Milesina vogesiaca	0,I
	Milesina whitei	0,I
	Pucciniastrum circaeae	0,I
	Pucciniastrum epilobii s.str.	0,I
	Pucciniastrum pustulatum?	0,I
	Pucciniastrum symphyti	0,I
	Uredinopsis filicina	0,I
	Uredinopsis pteridis?	0,I
	Uredinopsis struthiopteridis?	0,I

Host taxon	Rust taxon	Sori and spores
Abies spp. cult. (e.g., *A. balsamea*, *A. cephalonica*, *A. concolor*, *A. grandis*, *A. nordmanniana*, *A. pinsapo*, *A. sibirica*, *A. veitchii*)	*Calyptospora columnaris*	[0],I
	Hyalopsora aspidiotus	0,I
	Melampsora abietis-caprearum (*M. epitea* s.l.)	0,I
	Melampsorella elatina	0,I
	Milesina sp.	0,I
	Milesina blechni	0,I
	Milesina kriegeriana	0,I
	Milesina polypodii	0,I
	Milesina scolopendrii	0,I
	Milesina vogesiaca	0,I
	Pucciniastrum epilobii s.str.	0,I
	Pucciniastrum pustulatum?	0,I
	Uredinopsis filicina	0,I
	Uredinopsis pteridis	0,I
	Uredinopsis struthiopteridis	0,I
Adenostyles alliariae	***Coleosporium cacaliae*** auct.	Ib,III*
Adenostyles alpina (*A. glabra*)	***Coleosporium cacaliae*** auct.	Ib,III*
Adenostyles leucophylla	*Coleosporium cacaliae* auct.	Ib,III*
Adiantum capillus-veneris	*Hyalopsora adianti-capilli-veneris*	II, III
Agrimonia eupatoria	***Thekopsora agrimoniae***	II,III
Agrimonia procera	*Thekopsora agrimoniae*	II,III
Alchemilla* ser. *Pubescentes	***Trachyspora alchemillae***	I,III
Alchemilla ser. *Splendentes*	*Trachyspora alchemillae*	I,III
Alchemilla* ser. *Vulgares	***Trachyspora alchemillae***	I,III
Alchemilla alpina s. latiss.	***Trachyspora melospora***	[I],III
Alchemilla alpina?	*Trachyspora melospora*	[I],III
Alchemilla hoppeana	*Trachyspora melospora*	[I],III
Alchemilla pentaphyllea	*Trachyspora pentaphylleae*	[I],III
***Alchemilla* '*plicatula*'** [*A. alpigena* or *A. nitida*]	***Trachyspora melospora***	[I],III
Allium angulosum	*Melampsora* sp. (44) (*Caeoma* sp.)	0,I
Allium ascalonicum	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0,I
	Melampsora vitellinae	0,I
Allium carinatum	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Allium carinatum subsp. *pulchellum* (*A. pulchellum*)	*Melampsora allii-fragilis*	0,I
	Melampsora vitellinae	0,I
Allium cepa	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Allium fistulosum	*Melampsora allii-fragilis*	0,I
	Melampsora vitellinae	0,I
Allium flavum	***Melampsora vitellinae***	0,I
Allium lusitanicum (*A. senescens* subsp. *montanum*)	*Melampsora allii-fragilis*	0,I
	Melampsora vitellinae	0,I
Allium ochroleucum	*Melampsora allii-fragilis*	0,I
	Melampsora vitellinae	0,I
Allium oleraceum	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Allium rotundum	*Melampsora vitellinae*	0,I
Allium sativum	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Allium schoenoprasum	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
	Melampsora sp. (43) (*Caeoma* sp.)	0,I

Host taxon	Rust taxon	Sori and spores
Allium scorodoprasum	*Melampsora allii-populina*	0.I
	Melampsora vitellinae	0,I
	***Melampsora* sp.** (45) (*Caeoma* sp.)	0,I
Allium scorodoprasum?	*Melampsora allii-fragilis*	0,I
Allium sphaerocephalon	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Allium strictum	*Melampsora vitellinae*	0,I
Allium suaveolens	*Melampsora allii-populina*	0.I
	Melampsora vitellinae	0,I
Allium ursinum	***Melampsora allii-fragilis***	0,I
	Melampsora allii-populina	0,I
	Melampsora vitellinae	0,I
Allium victorialis	*Melampsora allii-fragilis*	0,I
	Melampsora vitellinae	0,I
Allium vineale	*Melampsora allii-fragilis*	0,I
	Melampsora allii-populina	0.I
	Melampsora vitellinae	0,I
Alnus alnobetula	*Melampsoridium betulinum*	II,III
Alnus glutinosa	*Melampsoridium betulinum*	II,III
	Melampsoridium hiratsukanum	II,III
Alnus glutinosa* × *incana	***Melampsoridium hiratsukanum***	II,III
Alnus incana	*Melampsoridium betulinum*	II,III
	Melampsoridium hiratsukanum	II,III
Amelanchier asiatica	*Gymnosporangium amelanchieris*	0,I
	Ochropsora anemones	II,III*
Amelanchier ovalis	***Gymnosporangium amelanchieris***	0,I
	Gymnosporangium clavariiforme	0,I
Anacamptis morio (*Orchis m.*)	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Anemone baldensis	***Tranzschelia* cf. *anemones***	0,III
Anemone coronaria cult.	***Tranzschelia discolor***	0,I
Anemone coronaria?	*Tranzschelia pruni-spinosae*	0,I
Anemone nemorosa	***Ochropsora anemones***	0,I
	***Tranzschelia anemones* s.str.**	0,III
Anemone nemorosa?	*Tranzschelia pruni-spinosae*	0,I
Anemone ranunculoides	***Ochropsora anemones***	0,I
	Tranzschelia pruni-spinosae	0,I
Anemone ranunculoides?	*Tranzschelia anemones*	0,III
Anemone trifolia	***Ochropsora anemones***	0,I
	***Tranzschelia anemones* s.str.**	0,III
Aposeris foetida	***Coleosporium aposeridis*** (*C. tussilaginis* s.l.)	Ib,III*
Arctostaphylos alpinus	***Pucciniastrum sparsum***	II,III
Arctostaphylos uva-ursi	***Pucciniastrum sparsum***	II,III
Arenaria serpyllifolia	*Melampsorella elatina*	II,III
***Arum* 'alpinum'** (*A. italicum*?, *A. cylindraceum*?)	***Melampsora allii-populina***	0.I
Arum maculatum	*Melampsora ari-salicina*	0,I
***Arum maculatum*?**	***Melampsora allii-populina***	0.I
Aruncus dioicus	***Ochropsora anemones***	II,III*
Asclepias syriaca	*Cronartium flaccidum*	II,III
Asperula purpurea	*Pucciniastrum guttatum*	II,III
Asplenium adiantum-nigrum	*Milesina magnusiana*	II
Asplenium ×alternifolium	*Milesina feurichii*	II,III
Asplenium ruta-muraria	***Milesina murariae***	II,III
Asplenium scolopendrium (*Phyllitis s.*)	***Milesina scolopendrii***	II,III
Asplenium septentrionale	***Milesina feurichii***	II,III
Athyrium filix-femina	*Hyalopsora polypodii*	II,II*,(III)
Bartsia alpina	*Coleosporium euphrasiae*	Ib,III*
Betula humilis	***Melampsoridium betulinum***	II,III
Betula nana	*Melampsoridium betulinum*	II,III
Betula papyrifera	*Melampsoridium betulinum*	II,III
Betula pendula	***Melampsoridium betulinum***	II,III

Host taxon	Rust taxon	Sori and spores
Betula pubescens	***Melampsoridium betulinum***	II,III
Calendula officinalis	*Coleosporium senecionis* (*C. calendulae*)	Ib,III*
Calluna vulgaris	*Thekopsora ericae*	II
Campanula barbata	***Coleosporium campanulae***	Ib,III*
Campanula beckiana	***Coleosporium campanulae***	Ib,III*
Campanula bononiensis	***Coleosporium campanulae***	Ib,III*
Campanula carnica	***Coleosporium campanulae***	Ib,III*
Campanula cervicaria	*Coleosporium campanulae*	Ib,III*
Campanula cespitosa	***Coleosporium campanulae***	Ib,III*
Campanula cochleariifolia	***Coleosporium campanulae***	Ib,III*
Campanula glomerata	***Coleosporium campanulae***	Ib,III*
Campanula latifolia	***Coleosporium campanulae***	Ib,III*
Campanula medium	*Coleosporium campanulae*	Ib,III*
Campanula moravica	***Coleosporium campanulae***	Ib,III*
Campanula patula s.l. (incl. subsp. *jahorinae*)	***Coleosporium campanulae***	Ib,III*
Campanula persicifolia	***Coleosporium campanulae***	Ib,III*
Campanula praesignis	***Coleosporium campanulae***	Ib,III*
Campanula pulla	*Coleosporium campanulae*	Ib,III*
Campanula rapunculoides	***Coleosporium campanulae***	Ib,III*
Campanula rapunculus	***Coleosporium campanulae***	Ib,III*
Campanula rhomboidalis	*Coleosporium campanulae*	Ib,III*
Campanula rotundifolia agg.	***Coleosporium campanulae***	Ib,III*
Campanula scheuchzeri	***Coleosporium campanulae***	Ib,III*
Campanula sibirica	*Coleosporium campanulae*	Ib,III*
Campanula thyrsoides	*Coleosporium campanulae*	Ib,III*
Campanula trachelium	***Coleosporium campanulae***	Ib,III*
Campanula witasekiana	***Coleosporium campanulae***	Ib,III*
Cannabis sativa	*Uredo kriegeriana*	II
Carpinus betulus	***Melampsoridium carpini***	II,III
Cerastium alpinum agg.	*Melampsorella elatina*	II,III
Cerastium arvense	***Melampsorella elatina***	II,III
Cerastium cerastoides → Dichodon c.		
Cerastium fontanum	***Melampsorella elatina***	II,III
Cerastium glomeratum	*Melampsorella elatina*	II,III
Cerastium glutinosum	*Melampsorella elatina*	II,III
Cerastium holosteoides	*Melampsorella elatina*	II,III
Cerastium latifolium	*Melampsorella elatina*	II,III
Cerastium pumilum	*Melampsorella elatina*	II,III
Cerastium semidecandrum	*Melampsorella elatina*	II,III
Cerinthe minor	***Coleosporium cerinthes***	Ib,III*
Chelidonium majus	***Melampsora magnusiana*** (*M. populnea* s.l.)	0,I
Chimaphila umbellata	*Pucciniastrum pyrolae*	II,III
Circaea alpina	***Pucciniastrum circaeae***	II,III
Circaea canadensis subsp. *quadrisulcata* (*C. lutetiana* subsp. *qu.*)	*Pucciniastrum circaeae*	II,III
Circaea ×intermedia (*C. alpina* × *lutetiana*)	***Pucciniastrum circaeae***	II,III
Circaea lutetiana	***Pucciniastrum circaeae***	II,III
Clematis sp. cult.	*Coleosporium tussilaginis* s.l.	Ib,III*
Colchicum autumnale	*Uredo colchici-autumnalis*	0?,II
Corydalis cava	***Melampsora magnusiana*** (*M. populnea* s.l.)	0,I
Corydalis intermedia	***Melampsora magnusiana*** (*M. populnea* s.l.)	0,I
Corydalis pumila	*Melampsora magnusiana* (*M. populnea* s.l.)	0,I
Corydalis solida	***Melampsora magnusiana*** (*M. populnea* s.l.)	0,I
Cotoneaster integerrimus	***Gymnosporangium confusum* s.str.**	0,I
Cotoneaster integerrimus?	***Gymnosporangium clavariiforme***	0,I
	Gymnosporangium fusisporum	0,I
Cotoneaster melanocarpus (*C. niger*)	*Gymnosporangium fusisporum*	0,I
	Gymnosporangium confusum s.str.	0,I
Cotoneaster tomentosus	*Gymnosporangium fusisporum*	0,I
Cotoneaster tomentosus?	*Gymnosporangium confusum* s.str.	0,I

Host taxon	Rust taxon	Sori and spores
Crataegus germanica (*Mespilus g.*)	*Gymnosporangium confusum* s.str.	0,I
Crataegus laevigata	*Gymnosporangium confusum* s.str.	0,I
	Gymnosporangium clavariiforme	0,I
Crataegus lindmanii (*C. rhipidophylla* subsp. *lindmanii*)	*Gymnosporangium clavariiforme*	0,I
Crataegus monogyna	***Gymnosporangium clavariiforme***	0,I
	Gymnosporangium confusum s.str.	0,I
Crepis tectorum	*Coleosporium sonchi*	Ib,III*
Cruciata laevipes	*Pucciniastrum guttatum*	II,III
Cruciata verna (*C. glabra*)	*Pucciniastrum guttatum*	II,III
Cydonia oblonga	*Gymnosporangium clavariiforme*	0,[I]
	Gymnosporangium confusum s.str.	0,I
	Gymnosporangium tremelloides	0,I
Cystopteris alpina	***Hyalopsora polypodii***	II,II*,(III)
Cystopteris fragilis	***Hyalopsora polypodii***	II,II*,(III)
Dactylorhiza fuchsii (*D. maculata* p.p.)	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Dactylorhiza incarnata [agg.]	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Dactylorhiza majalis	***Melampsora repentis*** (*M. epitea* s.l.)	0,I
Dactylorhiza sambucina	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Dactylorhiza traunsteineri	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Dasiphora fruticosa (*Potentilla f.*)	*Phragmidium andersonii*	0?,I–III
Dichodon cerastoides (*Cerastium c.*)	***Melampsorella elatina***	II,III
Doronicum austriacum	***Coleosporium doronici***	Ib,III*
Doronicum glaciale* subsp. *calcareum (*D. calcareum*)	***Coleosporium doronici***	Ib,III*
Dryopteris affinis [agg.]	***Milesina carpatica***	II,III
	Milesina kriegeriana	II,III
Dryopteris borreri (*D. affinis* agg.)	*Milesina kriegeriana*	II,III
Dryopteris carthusiana	***Milesina kriegeriana***	II,III
Dryopteris carthusiana agg.	*Milesina carpatica*	II,III
	Milesina kriegeriana	II,III
Dryopteris dilatata	*Milesina kriegeriana*	II,III
Dryopteris filix-mas	*Milesina carpatica*	II,III
	Milesina kriegeriana	II,III
Dryopteris filix-mas agg.	***Milesina carpatica***	II,III
	Milesina kriegeriana	II,III
Duchesnea indica → *Potentilla i.*		
Emilia sonchifolia cult.	***Coleosporium sonchi***	Ib,III*
Empetrum hermaphroditum	***Chrysomyxa empetri***	Ib,III
Empetrum nigrum	*Chrysomyxa empetri*	Ib,III
Epilobium alpestre	*Pucciniastrum pustulatum*	II,III
Epilobium alsinifolium	*Melampsora* sp. (40) (*Caeoma epilobii-alpini*)	0,I
	Pucciniastrum pustulatum	II,III
Epilobium anagallidifolium	*Pucciniastrum pustulatum*	II,III
Epilobium anagallidifolium?	*Melampsora* sp. (40) (*Caeoma epilobii-alpini*)	0,I
Epilobium angustifolium	***Pucciniastrum epilobii* s.str.**	II,III
Epilobium ciliatum	*Pucciniastrum pustulatum*	II,III
Epilobium collinum	***Pucciniastrum pustulatum***	II,III
Epilobium dodonaei	*Pucciniastrum epilobii* s.str.?	II,III
	Pucciniastrum epilobii-dodonaei	II,III
Epilobium fleischeri	*Pucciniastrum pustulatum*	II,III
Epilobium hirsutum	*Pucciniastrum pustulatum*	II,III
Epilobium montanum	***Pucciniastrum pustulatum***	II,III
Epilobium obscurum	*Pucciniastrum pustulatum*	II,III
Epilobium palustre	*Melampsora* sp. (40) (*Caeoma epilobii-alpini*)	0,I
	Pucciniastrum pustulatum	II,III
Epilobium parviflorum	***Pucciniastrum pustulatum***	II,III
Epilobium roseum	***Pucciniastrum pustulatum***	II,III
Epilobium tetragonum	***Pucciniastrum pustulatum***	II,III
Epilobium tetragonum subsp. *lamyi*	*Pucciniastrum pustulatum*	II,III
Epipactis helleborine	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Eranthis hyemalis cult.	***Leucotelium cerasi***	0,I
Erechtites hieraciifolius	*Coleosporium tussilaginis* s.l.	Ib,III*

Host taxon	Rust taxon	Sori and spores
Erica gracilis cult.	*Thekopsora ericae*	II
Erica hiemalis cult.	*Thekopsora ericae*	II
Euonymus europaeus	***Melampsora euonymi-caprearum*** (*M. epitea* s.l.)	0,I
Euonymus latifolius?	*Melampsora euonymi-caprearum* (*M. epitea* s.l.)	0,I
Euonymus verrucosus?	*Melampsora euonymi-caprearum* (*M. epitea* s.l.)	0,I
Euphorbia amygdaloides	***Melampsora euphorbiae*** s.l. (*M. euphorbiae-amygdaloidis*)	(0,I),II,(III?)
Euphorbia amygdaloides?	*Melampsora euphorbiae-helioscopiae* (*M. euphorbiae* s.l.)	0–III
Euphorbia angulata	***Melampsora euphorbiae-dulcis*** (*M. euphorbiae* s.l.)	0–III
Euphorbia angulata?	*Melampsora euphorbiae-helioscopiae* (*M. euphorbiae* s.l.)	0–III
Euphorbia austriaca → *E. illirica*		
Euphorbia carniolica	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	0–III
Euphorbia cyparissias	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia dulcis (incl. subsp. *purpurata*)	***Melampsora euphorbiae-dulcis*** (*M. euphorbiae* s.l.)	0–III
Euphorbia epithymoides (*E. polychroma*)	*Melampsora euphorbiae-helioscopiae* (*M. euphorbiae* s.l.)	0–III
Euphorbia esula	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia exigua	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia falcata	***Melampsora euphorbiae-gerardianae*** (*M. euphorbiae* s.l.)	II,III
	Melampsora gelmii (*M. euphorbiae* s.l.)	II,III
Euphorbia glareosa	*Melampsora euphorbiae* s.l.	0–III
Euphorbia glareosa?	*Melampsora euphorbiae-helioscopiae* (*M. euphorbiae* s.l.)	0–III
Euphorbia helioscopia	***Melampsora euphorbiae-helioscopiae*** (*M. euphorbiae* s.l.)	0–III
Euphorbia illirica (*E. austriaca*)	***Melampsora euphorbiae*** s.l.	(0,I),II,III
Euphorbia illirica (*E. villosa*)	*Melampsora euphorbiae* s.l.	0–III
Euphorbia illirica? (*E. villosa*)	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	0–III
Euphorbia lathyris	***Melampsora euphorbiae-dulcis*** (*M. euphorbiae* s.l.)	0–III
Euphorbia lucida	*Melampsora euphorbiae* s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia palustris	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia palustris?	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	0–III
Euphorbia peplus	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia platyphyllos	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	0–III
Euphorbia polychroma → *E. epithymoides*		
Euphorbia pulcherrima	*Melampsora euphorbiae* s.l.	II,III
Euphorbia salicifolia	*Melampsora euphorbiae* s.l.	0–III
Euphorbia salicifolia?	*Melampsora euphorbiae* s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia saxatilis	***Melampsora euphorbiae*** s.l.	II
Euphorbia seguieriana (*E. gerardiana*)	*Melampsora euphorbiae-gerardianae* (*M. euphorbiae* s.l.)	II,III
Euphorbia stricta	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	0–III
Euphorbia stricta?	*Melampsora euphorbiae* s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia verrucosa	***Melampsora euphorbiae*** s. Gäumann (*M. euphorbiae* s.l.)	0–III
Euphorbia villosa → *E. illirica*		
Euphorbia virgata	***Melampsora euphorbiae*** s.l.	(0,I),II,III
Euphorbia virgata?	*Melampsora euphorbiae-dulcis* (*M. euphorbiae* s.l.)	(0,I),II,(III)
Euphrasia hirtella	*Coleosporium euphrasiae*	Ib,III*
Euphrasia kerneri	*Coleosporium euphrasiae*	Ib,III*
Euphrasia micrantha	*Coleosporium euphrasiae*	Ib,III*
Euphrasia minima	*Coleosporium euphrasiae*	Ib,III*
Euphrasia nemorosa	*Coleosporium euphrasiae*	Ib,III*
Euphrasia nemorosa × *stricta*	*Coleosporium euphrasiae*	Ib,III*
Euphrasia officinalis (*E. rostkoviana* agg.)	***Coleosporium euphrasiae***	Ib,III*
Euphrasia officinalis agg. (*E. rostkoviana* agg.)	***Coleosporium euphrasiae***	Ib,III*
Euphrasia officinalis* subsp. *picta (*E. picta*)	***Coleosporium euphrasiae***	Ib,III*
Euphrasia salisburgensis	***Coleosporium euphrasiae***	Ib,III*
Euphrasia stricta agg.	***Coleosporium euphrasiae***	Ib,III*
Filipendula ulmaria [subsp. *ulmaria*]	***Triphragmium ulmariae***	0,IIa+b,III
Filipendula ulmaria subsp. *denudata*	*Triphragmium ulmariae*	0,IIa+b,III
Filipendula vulgaris	***Triphragmium filipendulae***	0,IIa+b,III
Fragaria vesca?	*Phragmidium fragariae*	0–III
Fragaria viridis?	*Phragmidium fragariae*	0–III
	Phragmidium tormentillae	II
***Fuchsia* sp.** cult.	***Pucciniastrum fuchsiae***	II
Fumaria officinalis	*Melampsora magnusiana* (*M. populnea* s.l.)	0,I
Galanthus nivalis	***Melampsora galanthi-fragilis***	0.I
Galium album	*Pucciniastrum guttatum*	II,III

Host taxon	Rust taxon	Sori and spores
Galium anisophyllon	*Pucciniastrum guttatum*	II,III
Galium aparine	*Pucciniastrum guttatum*	II,III
Galium aristatum	*Pucciniastrum guttatum*	II,III
Galium glaucum	*Pucciniastrum guttatum*	II,III
Galium intermedium (*G. schultesii*)	*Pucciniastrum guttatum*	II,III
Galium mollugo agg.	***Pucciniastrum guttatum***	II,III
Galium odoratum	***Pucciniastrum guttatum***	II,III
Galium palustre	*Pucciniastrum guttatum*	II,III
Galium parisiense	*Pucciniastrum guttatum*	II,III
Galium ×pomeranicum (*G. album* × *verum*)	*Pucciniastrum guttatum*	II,III
Galium pumilum	***Pucciniastrum guttatum***	II,III
Galium rivale	*Pucciniastrum guttatum*	II,III
Galium rotundifolium	*Pucciniastrum guttatum*	II,III
Galium saxatile	***Pucciniastrum guttatum***	II,III
Galium schultesii → *G. intermedium*		
Galium spurium	*Pucciniastrum guttatum*	II,III
Galium sylvaticum	***Pucciniastrum guttatum***	II,III
Galium uliginosum	*Pucciniastrum guttatum*	II,III
Galium verum	***Pucciniastrum guttatum***	II,III
Gentiana asclepiadea	***Cronartium flaccidum***	II,III
Godetia sp. cult.	*Pucciniastrum pustulatum*?	II,III
Goodyera repens	*Pucciniastrum goodyerae*	II
Gymnadenia conopsea	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Gymnocarpium dryopteris	***Hyalopsora aspidiotus***	II,II*,(III)
Gymnocarpium robertianum	***Hyalopsora aspidiotus***	II,II*,(III)
Hepatica nobilis?	*Tranzschelia pruni-spinosae*	0,I
Hypericum calycinum	***Melampsora* sp.** (46) (*Caeoma* sp.)	I
Hypericum dubium	*Melampsora hypericorum*	I,III
Hypericum elegans	*Melampsora hypericorum*	I,III
Hypericum hirsutum	***Melampsora hypericorum***	I,III
Hypericum humifusum	***Melampsora hypericorum***	I,III
	***Melampsora* sp.** (47) (*Uredo hyperici-humifusi*)	II
Hypericum maculatum	***Melampsora hypericorum***	I,III
Hypericum maculatum agg.	***Melampsora hypericorum***	I,III
Hypericum montanum	***Melampsora hypericorum***	I,III
Hypericum perforatum	***Melampsora hypericorum***	I,III
Hypericum pulchrum	*Melampsora hypericorum*	I,III
Hypericum tetrapterum	*Melampsora hypericorum*	I,III
Impatiens balsamina cult.	***Cronartium flaccidum***	II,III
Inula helenium	***Coleosporium inulae***	Ib,III*
Inula p.p. (*I. ensifolia, I. germanica, I. salicina*) → *Pentanema*		
Isopyrum thalictroides	***Triphragmiopsis isopyri***	III
***Juniperus* sp.**	***Gymnosporangium confusum* s.str.**	III
	Gymnosporangium fusisporum	III
Juniperus sect. *Juniperus*	*Gymnosporangium confusum* s.str.	III
Juniperus sect. *Sabina*	*Gymnosporangium confusum* s.str.	III
	Gymnosporangium fusisporum	III
Juniperus chinensis	***Gymnosporangium sabinae***	III
Juniperus communis	***Gymnosporangium amelanchieris***	III
	Gymnosporangium clavariiforme	III
	***Gymnosporangium cornutum* s.str.**	III
	Gymnosporangium torminali-juniperinum	III
	Gymnosporangium tremelloides	III
Juniperus communis subsp. *communis*	*Gymnosporangium gaeumannii* subsp. *gaeumannii*	II,[III]
Juniperus communis* subsp. *nana (subsp. *alpina*)	*Gymnosporangium amelanchieris*	III
	Gymnosporangium clavariiforme	III
	Gymnosporangium cornutum s.str.	III
	Gymnosporangium tremelloides	III
***Juniperus communis* subsp. *nana*?** (subsp. *alpina*)	***Gymnosporangium gaeumannii* subsp. *gaeumannii***	II,[III]
Juniperus sabina	***Gymnosporangium sabinae***	III
Juniperus virginiana	*Gymnosporangium sabinae*	III
Lactuca muralis (*Mycelis m.*)	*Coleosporium sonchi*	Ib,III*
Lapsana communis	*Coleosporium sonchi*	Ib,III*

Host taxon	Rust taxon	Sori and spores
Larix decidua	*Melampsora farinosa*	0,I
	Melampsora laricis-epitea (*M. epitea* s.l.)	0,I
	Melampsora laricis-pentandrae	0,I
	Melampsora laricis-populina	0,I
	Melampsora laricis-tremulae (*M. populnea* s.l.)	0,I
	Melampsoridium betulinum	0,I
	Melampsoridium hiratsukanum	0,I
Larix spp. cult. (e.g., *Larix kaempferi*)	*Melampsora farinosa*	0,I
	Melampsora laricis-epitea (*M. epitea* s.l.)	0,I
	Melampsora laricis-pentandrae	0,I
	Melampsora laricis-populina	0,I
	Melampsora laricis-tremulae (*M. populnea* s.l.)	0,I
	Melampsoridium betulinum	0,I
	Melampsoridium hiratsukanum	0,I
Ledum palustre → *Rhododendron tomentosum*		
Legousia hybrida	*Coleosporium campanulae*	Ib,III*
Legousia speculum-veneris	***Coleosporium campanulae***	Ib,III*
Leucojum vernum	***Melampsora* sp.** (41) (*Caeoma leucoji-verni*)	0,I
Ligularia sibirica	***Coleosporium ligulariae***	Ib,III*
Ligusticum mutellina → *Mutellina adonidifolia*		
Linum alpinum (*L. perenne* subsp. *alpinum*)	***Melampsora liniperda***	0–III
Linum austriacum	***Melampsora liniperda***	0–III
Linum catharticum	***Melampsora lini***	II,III
Linum flavum	*Melampsora liniperda*	0–III
Linum hirsutum	*Melampsora liniperda*	0–III
Linum maritimum	*Melampsora liniperda*	0–III
Linum perenne s. strictiss.	*Melampsora liniperda*	0–III
Linum tenuifolium	*Melampsora liniperda*	0–III
Linum usitatissimum	***Melampsora liniperda***	0–III
Linum viscosum	*Melampsora liniperda*	0–III
Listera ovata → *Neottia o.*		
Lobelia cardinalis	***Coleosporium campanulae***	Ib,III*
Malus baccata	*Gymnosporangium tremelloides*	0,I
Malus domestica	*Gymnosporangium clavariiforme*	0,[I]
	Gymnosporangium tremelloides	0,I
	Ochropsora anemones	II,III*
Malus sylvestris	*Gymnosporangium tremelloides*	0,I
	Ochropsora anemones	II,III*
Matteuccia struthiopteris	***Uredinopsis struthiopteridis***	II,II*,III
Melampyrum arvense	***Coleosporium melampyri***	Ib,III*
	Cronartium flaccidum	II,III
Melampyrum cristatum	*Coleosporium melampyri*	Ib,III*
	Cronartium flaccidum	II,III
Melampyrum nemorosum	***Coleosporium melampyri***	Ib,III*
Melampyrum nemorosum agg.	***Coleosporium melampyri***	Ib,III*
Melampyrum pratense	***Coleosporium melampyri***	Ib,III*
Melampyrum sylvaticum	***Coleosporium melampyri***	Ib,III*
	Cronartium flaccidum	II,III
Mercurialis annua	*Melampsora pulcherrima* (*M. populnea* s.l.)	0,I
Mercurialis perennis	***Melampsora rostrupii*** (*M. populnea* s.l.)	0,I
Mespilus germanica → *Crataegus g.*		
Meum athamanticum	*Nyssopsora echinata*	III
Moehringia trinervia	*Melampsorella elatina*	II,III
Moneses uniflora	***Pucciniastrum pyrolae***	II,III
	Rossmanomyces monesis	Ib,III
	Rossmanomyces pyrolae	Ib,III
Muscari comosum	*Melampsora allii-populina*	0.I
***Muscari neglectum*?**	***Melampsora allii-populina***	0.I
Mutellina adonidifolia (*Ligusticum mutellina*)	***Nyssopsora echinata***	III
Mycelis muralis → *Lactuca m.*		
Myosotis laxa [subsp. *cespitosa*] (*M. palustris* agg.)	*Cronartium flaccidum*	II,III
Myosotis palustris agg.	***Pucciniastrum brachybotrydis***	II,III

Host taxon	Rust taxon	Sori and spores
Myosoton aquaticum → *Stellaria aquatica*		
Neotinea ustulata (*Orchis u.*)	***Melampsora repentis*** (*M. epitea* s.l.)	0,I
Neottia ovata (*Listera o.*)	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Odontites luteus	*Coleosporium euphrasiae*	Ib,III*
***Odontites vernus*?**	***Coleosporium euphrasiae***	Ib,III*
Odontites vulgaris (*O. ruber* p.p.)	***Coleosporium euphrasiae***	Ib,III*
Odontites vulgaris agg. (*O. ruber* agg.)	***Coleosporium euphrasiae***	Ib,III*
Omphalodes [sp.]	*Pucciniastrum brachybotrydis*	II,III
Ophrys insectifera	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Ophrys sphegodes (*O. sphecodes*)	***Melampsora repentis*** (*M. epitea* s.l.)	0,I
Orchis mascula [s.l.]	***Melampsora repentis*** (*M. epitea* s.l.)	0,I
Orchis militaris	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Orchis morio → *Anacamptis m.*		
Orchis purpurea	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Orchis ustulata → *Neotinea u.*		
Orthilia secunda	***Pucciniastrum pyrolae***	II,III
	Rossmanomyces ramischiae	Ia+b,III
***Paeonia* sp.** cult.	***Cronartium flaccidum***	II,III
Papaver dubium [s.l.]	*Melampsora magnusiana* (*M. populnea* s.l.)	0,I
Pedicularis palustris	*Coleosporium euphrasiae*	Ib,III*
	Cronartium flaccidum	II,III
Pedicularis sceptrum-carolinum	*Cronartium flaccidum*	II,III
Pentanema ensifolium (*Inula ensifolia*)	***Coleosporium inulae***	Ib,III*
Pentanema germanicum (*Inula germanica*)	***Coleosporium inulae***	Ib,III*
Pentanema salicinum (*Inula salicina*)	***Coleosporium inulae***	Ib,III*
Pericallis cruenta cv. (*Senecio cruentus*)	*Coleosporium senecionis*	Ib,III*
Petasites albus	***Coleosporium petasitis***	Ib,III*
Petasites hybridus	***Coleosporium petasitis***	Ib,III*
Petasites paradoxus	***Coleosporium petasitis***	Ib,III*
Phegopteris connectilis (*Thelypteris phegopteris*)	***Uredinopsis filicina***	II,II*,III
Phyllitis scolopendrium → *Asplenium s.*		
Phyteuma betonicifolium	***Coleosporium campanulae***	Ib,III*
Phyteuma nigrum	*Coleosporium campanulae*	Ib,III*
Phyteuma orbiculare	***Coleosporium campanulae***	Ib,III*
Phyteuma spicatum	***Coleosporium campanulae***	Ib,III*
Picea [sp.]	*Rossmanomyces monesis*	0,Ia
Picea abies	***Chrysomyxa abietis***	III
	Chrysomyxa empetri?	0,Ia
	Chrysomyxa ledi	0,Ia
	Chrysomyxa rhododendri	0,Ia
	Chrysomyxa woroninii	0,Ia
	Pucciniastrum sparsum	0,I
	Rossmanomyces pyrolae	0,Ia
	Thekopsora areolata	0,I
Picea abies?	*Chrysomyxa empetri*	0,Ia
Picea spp. cult. (e.g., *P. engelmannii*, *P. glauca*, *P. mariana*, *P. pungens*, *P. sitchensis*)	*Chrysomyxa abietis* *Chrysomyxa empetri* *Chrysomyxa ledi* *Chrysomyxa rhododendri* *Chrysomyxa woroninii* *Rossmanomyces monesis* *Rossmanomyces pyrolae*	
Pinus aristata	*Cronartium ribicola*	0,I
Pinus cembra	*Cronartium ribicola*	0,I
***Pinus flexilis*?**	***Cronartium ribicola***	0,I
Pinus koraiensis	*Cronartium ribicola*	0,I
Pinus monticola	*Cronartium ribicola*	0,I
Pinus mugo	***Coleosporium tussilaginis*** s.l.	0,Ia
	Cronartium flaccidum	0,I
	Cronartium pini	0,I
	Melampsora pinitorqua (*M. populnea* s.l.)	0,I
Pinus nigra	***Coleosporium tussilaginis*** s.l.	0,Ia
	Cronartium pini	0,I

Host taxon	Rust taxon	Sori and spores
Pinus peuce	*Cronartium ribicola*	0,I
Pinus ×rotundata auct. → *P. uliginosa*		
Pinus strobus	***Cronartium ribicola***	0,I
Pinus sylvestris	***Coleosporium tussilaginis*** s.l.	0,Ia
	Cronartium flaccidum	0,I
	Cronartium pini	0,I
	Melampsora pinitorqua (*M. populnea* s.l.)	0,I
Pinus uliginosa (*P. ×rotundata* auct.)	*Cronartium flaccidum*	0,I
	Melampsora pinitorqua (*M. populnea* s.l.)	0,I
Pinus wallichiana	*Cronartium ribicola*	0,I
Pinus spp. cult. (e.g., *P. aristata*, *P. koraiensis*, *P. monticola*, *P. peuce*, *P. wallichiana*)	*Cronartium ribicola*	0,I
Platanthera bifolia [agg.]	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Platanthera chlorantha	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Polypodium interjectum	***Milesina polypodii***	II,III
Polypodium vulgare [agg.]	***Milesina polypodii***	II,III
Polystichum aculeatum	*Milesina exigua*	II,III
	Milesina vogesiaca	II,III
	Milesina whitei	II,III
Polystichum braunii	***Milesina exigua***	II,III
Polystichum lonchitis	***Milesina vogesiaca***	II,III
Polystichum setiferum	*Milesina vogesiaca*	II,III
	Milesina whitei	II,III
Populus spp.	*Melampsora medusae*	II,(III)
Populus alba	***Melampsora laricis-tremulae*** (*M. populnea* s.l.)	II,III
	Melampsora populnea s.l.	II
	Melampsora pulcherrima	II,III
	Melampsora rostrupii	II,III
***Populus alba*?**	***Melampsora magnusiana***	II,(III)
	Melampsora pinitorqua	II,III
Populus balsamifera	*Melampsora laricis-tremulae* (*M. populnea* s.l.)	II,III
	Melampsora rostrupii (*M. populnea* s.l.)	II,III
	Melampsora allii-populina	II,III
	Melampsora laricis-populina	II,III
Populus ×canadensis (*P. deltoides × nigra*)	*Melampsora rostrupii* (*M. populnea* s.l.)	II,III
	Melampsora allii-populina	II,III
	Melampsora laricis-populina	II,III
Populus ×canescens (*P. alba × tremula*)	*Melampsora laricis-tremulae* (*M. populnea* s.l.)	II,III
	Melampsora pinitorqua (*M. populnea* s.l.)	II,III
	Melampsora rostrupii (*M. populnea* s.l.)	II,III
Populus deltoides	*Melampsora laricis-populina*	II,III
Populus deltoides?	*Melampsora allii-populina*	II,III
Populus gileadensis	***Melampsora laricis-populina***	II,III
Populus nigra	***Melampsora allii-populina***	II,III
	Melampsora laricis-populina	II,III
***Populus nigra*?**	***Melampsora magnusiana*** (*M. populnea* s.l.)	II,(III)
	Melampsora rostrupii (*M. populnea* s.l.)	II,III
Populus nigra* cv. *italica	*Melampsora allii-populina*	II,III
	Melampsora laricis-populina	II,III
	Melampsora rostrupii (*M. populnea* s.l.)	II,III
Populus simonii	*Melampsora allii-populina*	II,III
Populus tremula	***Melampsora laricis-tremulae*** (*M. populnea* s.l.)	II,III
	Melampsora pinitorqua (*M. populnea* s.l.)	II,III
	Melampsora rostrupii (*M. populnea* s.l.)	II,III
***Populus tremula*?**	***Melampsora magnusiana*** (*M. populnea* s.l.)	(II),III
Potentilla alba	***Phragmidium fragariae***	0–III
Potentilla anglica	*Phragmidium potentillae*	0–III
Potentilla anglica?	***Phragmidium tormentillae***	0,IIa+b,III
Potentilla arenaria → *P. incana*		
Potentilla argentea	***Phragmidium potentillae***	0–III
***Potentilla argentea*?**	***Phragmidium fragariae***	0–III

Host taxon	Rust taxon	Sori and spores
Potentilla aurea	***Phragmidium potentillae***	0–III
Potentilla brauneana	*Phragmidium potentillae*	0–III
Potentilla caulescens	***Phragmidium potentillae***	0–III
***Potentilla caulescens*?**	***Phragmidium fragariae***	0–III
Potentilla collina [agg.] (incl. *P. wiemanniana*)	*Phragmidium potentillae*	0–III
Potentilla crantzii s.l.	***Phragmidium potentillae***	0–III
Potentilla erecta	*Phragmidium potentillae*	0–III
	Phragmidium tormentillae	0,IIa+b,III
Potentilla fruticosa → *Dasiphora f.*		
Potentilla heptaphylla	***Phragmidium potentillae***	0–III
Potentilla incana (*P. arenaria*)	***Phragmidium potentillae***	0–III
Potentilla inclinata	***Phragmidium potentillae***	0–III
Potentilla indica (*Duchesnea i.*)	***Phragmidium duchesneae***	(0,IIa),IIb,III
Potentilla ×italica	*Phragmidium tormentillae*	0,IIa+b,III
***Potentilla ×italica*?**	***Phragmidium potentillae***	0–III
Potentilla leucopolitana	*Phragmidium potentillae*	0–III
Potentilla micrantha	***Phragmidium fragariae***	0–III
	Phragmidium potentillae	0–III
Potentilla micrantha* subsp. *carniolica	***Phragmidium fragariae***	0–III
Potentilla neglecta	*Phragmidium potentillae*	0–III
Potentilla neumanniana → *P. verna*		
Potentilla nivea (*P. prostrata* [subsp. *floccosa*])	*Phragmidium potentillae*	0–III
Potentilla norvegica	*Phragmidium potentillae*	0–III
Potentilla patula	*Phragmidium potentillae*	0–III
Potentilla prostrata [subsp. *floccosa*] → *P. nivea*		
Potentilla pusilla	***Phragmidium potentillae***	0–III
Potentilla recta [agg.]	***Phragmidium potentillae***	0–III
	Phragmidium tormentillae	0,IIa+b,III
Potentilla reptans	***Phragmidium potentillae***	(0–)III
	Phragmidium tormentillae	0,IIa+b,III
Potentilla sterilis	***Phragmidium fragariae***	0–III
Potentilla sterilis?	*Phragmidium potentillae*	0–III
Potentilla supina	*Phragmidium potentillae*	0–III
Potentilla verna [s.str.] (*P. neumanniana*)	*Phragmidium potentillae*	0–III
Potentilla verna agg.	***Phragmidium potentillae***	0–III
Potentilla wiemanniana → *P. collina* agg.		
Prunus armeniaca	*Leucotelium cerasi*	II,III
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus avium	*Ochropsora* anemones	II,III*
	Thekopsora areolata	II,[III]
	Tranzschelia discolor	II,III
***Prunus avium*?**	***Leucotelium cerasi***	II,III
Prunus cerasifera	*Leucotelium cerasi*	II,III
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus cerasus	*Leucotelium cerasi*	II,III
	Thekopsora areolata	II,[III]
Prunus domestica	***Leucotelium cerasi***	II,III
	Thekopsora areolata	II,[III]
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus dulcis	*Leucotelium cerasi*	II,III
	Tranzschelia discolor	II,III
Prunus fruticosa	*Leucotelium cerasi*	II,III
Prunus insititia	*Thekopsora areolata*	II,[III]
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus mahaleb	*Thekopsora areolata*	II,[III]
	Tranzschelia discolor	II,III
Prunus padus	*Leucotelium cerasi*	II,III
	***Ochropsora* anemones**	II,III*
	Thekopsora areolata	II,III

Host taxon	Rust taxon	Sori and spores
Prunus padus subsp. *petraea* (subsp. *borealis*)	*Thekopsora areolata*	II,[III]
Prunus persica	*Leucotelium cerasi*	II,III
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus pumila* var. *depressa cult.	***Leucotelium cerasi***	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus serotina	*Thekopsora areolata*	II,[III]
Prunus spinosa	*Leucotelium cerasi*	II,III
	Thekopsora areolata	II,[III]
	Tranzschelia pruni-spinosae	II,III
***Prunus spinosa*?**	***Tranzschelia discolor***	II,III
Prunus tenella	***Leucotelium cerasi***	II,III
	Ochropsora anemones	II,III*
	Tranzschelia discolor	II,III
	Tranzschelia pruni-spinosae	II,III
Prunus virginiana	*Leucotelium cerasi*	II,III
	Thekopsora areolata	II,III
	Tranzschelia pruni-spinosae	II,III
Pseudolarix amabilis	*Melampsora farinosa*	0,I
Pseudorchis albida	*Melampsora repentis* (*M. epitea* s.l.)	0,I
Pteridium aquilinum	*Uredinopsis pteridis*	II,II*,III
Pulsatilla alpina [s.l.]	*Coleosporium pulsatillae*	Ib,III*
Pulsatilla grandis	***Coleosporium pulsatillae***	Ib,III*
	Tranzschelia pulsatillae	[0],III
Pulsatilla oenipontana	***Coleosporium pulsatillae***	Ib,III*
Pulsatilla pratensis* subsp. *nigricans	***Coleosporium pulsatillae***	Ib,III*
	Tranzschelia pulsatillae	[0],III
Pulsatilla styriaca	***Coleosporium pulsatillae***	Ib,III*
	Tranzschelia pulsatillae	[0],III
Pulsatilla vernalis	*Coleosporium pulsatillae*	Ib,III*
	Tranzschelia pulsatillae	[0],III
Pulsatilla vulgaris [agg.]	***Coleosporium pulsatillae***	Ib,III*
	Tranzschelia pulsatillae	[0],III
Pyracantha coccinea	*Gymnosporangium amelanchieris*	0,I
	Gymnosporangium clavariiforme	0,I
	Gymnosporangium confusum s.str.	0,I
Pyrola chlorantha	***Pucciniastrum pyrolae***	II,III
	Rossmanomyces pyrolae	Ib,III
Pyrola media	*Pucciniastrum pyrolae*	II,III
	Rossmanomyces pyrolae	Ib,III
Pyrola minor	*Rossmanomyces pyrolae*	Ib,III
	Pucciniastrum pyrolae	II,III
Pyrola rotundifolia	***Pucciniastrum pyrolae***	II,III
	Rossmanomyces pyrolae	Ib,III
Pyrus communis	*Gymnosporangium confusum* s.str.	0,I
	Gymnosporangium clavariiforme	0,I
	Gymnosporangium sabinae	0,I
	Ochropsora anemones	II,III*
Pyrus pyraster	*Gymnosporangium sabinae*	0,I
Pyrus salviifolia	*Gymnosporangium sabinae*	0,I
Pyrus ×nivalis	*Gymnosporangium sabinae*	0,I
Quercus petraea	*Cronartium quercus*	II,III?
Quercus pubescens	*Cronartium quercus*	II,III?
Quercus robur	*Cronartium quercus*	II,III?
Rabelera holostea (*Stellaria h.*)	***Melampsorella elatina***	II,III
Rhinanthus alectorolophus agg.	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus aristatus agg.	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus buccalis (*R. alectorolophus* agg.)	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus ×digeneus (Janchen 1958: *R. alpinus* [*riphaeus*?] × *alectorolophus* var. *buccalis*)	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus glacialis (*R. aristatus* agg.)	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus minor	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus riphaeus (*R. pulcher*)	*Coleosporium euphrasiae*	Ib,III*

Host taxon	Rust taxon	Sori and spores
Rhinanthus serotinus	***Coleosporium euphrasiae***	Ib,III*
Rhinanthus serotinus agg.	***Coleosporium euphrasiae***	Ib,III*
Rhododendron spp. cult.	*Chrysomyxa rhododendri*	Ib,III
Rhododendron ferrugineum	***Chrysomyxa rhododendri***	Ib,III
Rhododendron hirsutum	***Chrysomyxa rhododendri***	Ib,III
Rhododendron tomentosum? (*Ledum palustre*)	*Chrysomyxa ledi*	Ib,III
Rhododendron tomentosum (*Ledum palustre*)	*Chrysomyxa woroninii*	Ib,III
Rhododendron ×intermedium	*Chrysomyxa rhododendri*	Ib,III
Ribes alpinum	***Cronartium ribicola***	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
Ribes aureum	***Cronartium ribicola***	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
Ribes nigrum	***Cronartium ribicola***	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
Ribes petraeum	*Cronartium ribicola*	II,III
Ribes rubrum	***Cronartium ribicola***	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
Ribes rubrum agg.	***Cronartium ribicola***	II,III
Ribes sanguineum	*Cronartium ribicola*	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
Ribes spicatum	*Cronartium ribicola*	II,III
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
Ribes uva-crispa	***Cronartium ribicola***	II,III
Ribes uva-crispa	*Melampsora ribis-epitea* (*M. epitea* s.l.)	0,I
Ribes uva-crispa	*Melampsora ribis-purpureae* (*M. epitea* s.l.)	0,I
Ribes uva-crispa	*Melampsora ribis-viminalis*	0,I
Ribes uva-crispa s.l.	***Cronartium ribicola***	II,III
Ribes uva-crispa s.l.	***Melampsora ribis-purpureae*** (*M. epitea* s.l.)	0,I
Ribes uva-crispa subsp. *grossularia*	*Melampsora ribis-epitea* (*M. epitea* s.l.)	0,I
	Melampsora ribis-purpureae (*M. epitea* s.l.)	0,I
	Melampsora ribis-viminalis	0,I
***Rosa* sp.** cult.	***Phragmidium mucronatum***	0–III
	Phragmidium tuberculatum	0–III
Rosa agrestis	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa ×alba cv.	***Phragmidium mucronatum***	0–III
Rosa arvensis	***Phragmidium mucronatum***	0–III
	Phragmidium tuberculatum	0–III
Rosa balsamica s.str. (*R. obtusifolia*, *R. tomentella*)	*Phragmidium tuberculatum*	0–III
Rosa canina s.l. (incl. *R. corymbifera*)	***Phragmidium mucronatum***	0–III
	Phragmidium rosae-pimpinellifoliae	0–III
	Phragmidium tuberculatum	0–III
Rosa centifolia (incl. f. *muscosa*) [cult.]	***Phragmidium mucronatum***	0–III
	Phragmidium tuberculatum	0–III
Rosa coriifolia → *R. dumalis* s.l.		
Rosa corymbifera → *R. canina* s.l.		
Rosa ×damascena cv.	*Phragmidium mucronatum*	0–III
Rosa dumalis s.l. (*R. coriifolia*, *R. vosagiaca*)	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa elliptica	*Phragmidium mucronatum*	0–III
Rosa foetida	*Phragmidium mucronatum*	0–III
	Phragmidium rosae-pimpinellifoliae	0–III

Host taxon	Rust taxon	Sori and spores
Rosa gallica	***Phragmidium mucronatum***	0–III
	Phragmidium tuberculatum	0–III
Rosa glauca	*Phragmidium rosae-pimpinellifoliae*	0–III
	Phragmidium tuberculatum	0–III
***Rosa glauca*?**	***Phragmidium fusiforme***	0–III
Rosa inodora	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa jundzillii → *R. marginata*		
Rosa lucida → *R. virginiana*		
Rosa majalis	*Phragmidium fusiforme*	0–III
	Phragmidium kamtschatkae	0,III
	Phragmidium mucronatum	0–III
	Phragmidium rosae-pimpinellifoliae	0–III
	Phragmidium tuberculatum	0–III
Rosa marginata (*R. jundzillii*)	*Phragmidium mucronatum*	0–III
Rosa micrantha	*Phragmidium mucronatum*	0–III
Rosa mollissima (*R. mollis*?, *R. villosa* agg.)	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa moschata (cv.?)	*Phragmidium mucronatum*	0–III
Rosa multiflora	*Phragmidium tuberculatum*	0–III
Rosa muscosa → *R. centifolia* f. *muscosa*		
Rosa obtusifolia → *R. balsamica*		
Rosa pendulina	***Phragmidium fusiforme***	0–III
Rosa pimpinellifolia → *R. spinosissima*		
Rosa rubiginosa	*Phragmidium mucronatum*	0–III
	Phragmidium rosae-pimpinellifoliae	0–III
	Phragmidium tuberculatum	0–III
Rosa rugosa	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa sherardii (*R. villosa* agg.)	*Phragmidium tuberculatum*	0–III
***Rosa spinosissima*?** (*R. pimpinellifolia*)	***Phragmidium rosae-pimpinellifoliae***	0–III
	Phragmidium mucronatum	0–III
Rosa tomentosa (*R. villosa* agg.)	***Phragmidium mucronatum***	0–III
	Phragmidium tuberculatum	0–III
***Rosa* ×*turbinata* cv.** (*R.* ×*francofurtana*?)	***Phragmidium mucronatum***	0–III
	Phragmidium mucronatum	0–III
Rosa villosa	*Phragmidium fusiforme*	0–III
	Phragmidium mucronatum	0–III
	Phragmidium tuberculatum	0–III
Rosa virginiana (*R. lucida*)	*Phragmidium mucronatum*	0–III
	Phragmidium tuberculatum	0–III
Rosa vosagiaca → *R. dumalis* s.l.		
***Rubus* sp.**	***Phragmidium candicantium***	II,III
***Rubus* sp.** (*R.* '*fuscus*')	***Phragmidium violaceum***	0–III
Rubus* sect. *Corylifolii	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
Rubus* sect. *Rubus	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium rubi	0–III
Rubus* ser. *Discolores	*Phragmidium candicantium*	II,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus albiflorus	*Phragmidium violaceum*	0–III
Rubus apricus	***Phragmidium violaceum***	0–III
Rubus bellardii (p.p.) → *R. pedemontanus*		
Rubus bifrons	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus caesius	***Phragmidium rubi***	0–III
	Phragmidium violaceum	0–III
Rubus caesius?	*Kuehneola uredinis*	0,IIa+b,III

Host taxon	Rust taxon	Sori and spores
Rubus canescens	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium candicantium	II,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus clusii	***Kuehneola uredinis***	0,IIa+b,III
Rubus constrictus (*R. vestii*)	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium candicantium	II,III
	Phragmidium violaceum	0–III
Rubus elatior	*Phragmidium violaceum*	0–III
Rubus ferox	***Kuehneola uredinis***	0,IIa+b,III
Rubus '***fruticosus*** agg.'	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus fuscus	*Kuehneola uredinis*	0,IIa+b,III
Rubus '*fuscus*' → *Rubus* sp.		
Rubus grabowskii (*R. thyrsanthus*)	*Phragmidium candicantium*	II,III
	Phramidium violaceum	0–III
Rubus gracilis	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus '*gremlii*' → *R. clusii*		
Rubus hirtus	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium violaceum	0–III
Rubus idaeus	***Phragmidium rubi-idaei***	0–III
Rubus laciniatus cv.	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium violaceum	0–III
Rubus macrophyllus	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium violaceum	0–III
Rubus montanus	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium candicantium	II,III
	Phragmidium violaceum	0–III
Rubus nemoralis	*Phragmidium violaceum*	0–III
Rubus nessensis	***Phragmidium rubi***	0–III
Rubus obtusangulus	*Phragmidium violaceum*	0–III
Rubus pedemontanus (*R. bellardii* p.p.)	***Kuehneola uredinis***	0,IIa+b,III
	Phragmidium violaceum	0–III
Rubus phyllostachys	*Phragmidium violaceum*	0–III
Rubus plicatus	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus praecox	*Phragmidium violaceum*	0–III
Rubus radula	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus rudis	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus salzmannii	***Kuehneola uredinis***	0,IIa+b,III
Rubus saxatilis	*Gymnoconia peckiana*	0,I,III
	Phragmidium acuminatum	0?,I–III
Rubus sprengelii	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium rubi	0–III
	Phragmidium violaceum	0–III
Rubus styriacus	***Kuehneola uredinis***	0,IIa+b,III
Rubus sulcatus	*Phragmidium rubi*	0–III
	Phragmidium violaceum	0–III
Rubus thyrsanthus → *R. grabowskii*		
Rubus ulmifolius	*Phragmidium rubi*	0–III
	Phragmidium violaceum	0–III

Host taxon	Rust taxon	Sori and spores
Rubus vestii → *R. constrictus*		
Rubus vestitus	*Kuehneola uredinis*	0,IIa+b,III
	Phragmidium violaceum	0–III
Rubus widderi	***Kuehneola uredinis***	0,IIa+b,III
Salix alba	*Melampsora epitea* s.l.	II,III
	Melampsora vitellinae	II,III
Salix alba × *babylonica*	*Melampsora vitellinae*	II,III
Salix alba × *fragilis* (*S.* ×*rubens*)	*Melampsora allii-fragilis*	II,(III)
	Melampsora vitellinae	II,III
Salix alba × *triandra*	*Melampsora vitellinae*	II,III
Salix alpina (*S. myrsinites* agg.)	***Melampsora epitea*** s.l.	II,III
***Salix alpina*?** (*S. myrsinites* agg.)	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
Salix appendiculata	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,III
	Melampsora farinosa	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
***Salix appendiculata*?**	***Melampsora epitea*** s.l.	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,(III)
Salix arbuscula agg. → auch *S. foetida*, *S. waldsteiniana*		
Salix arbuscula agg.	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
Salix aurita	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,III
	Melampsora repentis (*M. epitea* s.l.)	II,III
***Salix aurita*?**	***Melampsora euonymi-caprearum*** (*M. epitea* s.l.)	II,III
	Melampsora farinosa	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
Salix aurita × *repens*	*Melampsora farinosa*	II,III
	Melampsora epitea s.l.	II,III
Salix bicolor	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix breviserrata (*S. myrsinites* agg.)	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
Salix caesia	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix ×*calodendron* (*S. cinerea* × ?*viminalis*)	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix caprea	***Melampsora abietis-caprearum*** (*M. epitea* s.l.)	II,III
	Melampsora euonymi-caprearum (*M. epitea* s.l.)	II,III
	Melampsora farinosa	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
***Salix caprea*?**	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,(III)
	Melampsora repentis (*M. epitea* s.l.)	II,III
Salix cinerea	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
***Salix cinerea*?**	***Melampsora farinosa***	II,(III)
	Melampsora euonymi-caprearum (*M. epitea* s.l.)	II,III
Salix cinerea × *viminalis*	*Melampsora farinosa*	II,III
Salix daphnoides	*Melampsora farinosa*	II,(III)
	Melampsora ribis-purpureae (*M. epitea* s.l.)	II,[III]
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
Salix ×*dasyclados* (*S. caprea* × *cinerea* × *viminalis*)	*Melampsora farinosa*	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
Salix eleagnos (*S. elaeagnos*)	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,III
	Melampsora euonymi-caprearum (*M. epitea* s.l.)	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
Salix eleagnos? (*S. elaeagnos*)	*Melampsora repentis* (*M. epitea* s.l.)	II,III
Salix foetida (*S. arbuscula* agg.)	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,([III])
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
Salix fragilis	*Melampsora laricis-pentandrae*	II
	Melampsora allii-fragilis	II,(III)
	Melampsora ari-salicina	II,III
	Melampsora galanthi-fragilis	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III

Host taxon	Rust taxon	Sori and spores
Salix fragilis × *pentandra*	*Melampsora laricis-pentandrae*	II,III
Salix glabra	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
Salix glaucosericea	*Melampsora epitea* s.l.	II,III
Salix glaucosericea × *myrsinifolia*	*Melampsora epitea* s.l.	II,III
Salix hastata	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix hastata (and hybrids)	*Melampsora reticulatae* (*M. epitea* s.l.)	II,III
Salix hastata × *herbacea*	*Melampsora epitea* s.l.	II,III
Salix hastata × *myrsinifolia*	*Melampsora epitea* s.l.	II,III
Salix hegetschweileri	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix helvetica	*Melampsora abietis-caprearum*	II,([III])
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
Salix herbacea	***Melampsora arctica*** (*M. epitea* s.l.)	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
Salix lapponum [agg.]	*Melampsora lapponum* (*M. epitea* s.l.)	II,III
Salix myrsinifolia (*S. nigricans* agg.)	***Melampsora abietis-caprearum*** (*M. epitea* s.l.)	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)
Salix myrsinifolia? (*S. nigricans* agg.)	*Melampsora ribis-purpureae* (*M. epitea* s.l.)	II,III
Salix myrsinites agg.	*Melampsora arctica* (*M. epitea* s.l.)	II,III
Salix myrtilloides	*Melampsora reticulatae* (*M. epitea* s.l.)	II,III
	Melampsora sp. (38)	II,III
Salix nigricans agg. (incl. *S. mielichhoferi*, *S. myrsinifolia*)	***Melampsora epitea*** s.l.	II,III
Salix pentandra	*Melampsora allii-fragilis*	II,(III)
	Melampsora amygdalinae	0–III
	Melampsora galanthi-fragilis	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora laricis-pentandrae	II,III
	Melampsora vitellinae	II,III
Salix purpurea	*Melampsora abietis-caprearum*	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-purpureae (*M. epitea* s.l.)	II,III
Salix purpurea?	*Melampsora repentis*	II,III
Salix purpurea × *viminalis*	*Melampsora ribis-purpureae* (*M. epitea* s.l.)	II,III
Salix repens	***Melampsora repentis*** (*M. epitea* s.l.)	II,III
	Melampsora abietis-caprearum	II,III
Salix repens?	*Melampsora farinosa*	II,III
Salix repens subsp. *rosmarinifolia*	*Melampsora repentis* (*M. epitea* s.l.)	II,III
Salix reticulata	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
	Melampsora reticulatae (*M. epitea* s.l.)	II,III
Salix retusa	*Melampsora arctica*	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora reticulatae (*M. epitea* s.l.)	II,III
	Melampsora vitellinae	II,III
Salix serpyllifolia (*S. retusa agg.*)	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
***Salix ×smithiana*?** (*S. caprea* × *viminalis*)	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,(III)
	Melampsora euonymi-caprearum (*M. epitea* s.l.)	II
	Melampsora farinosa	II,III
Salix ×stipularis?	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,III
	Melampsora repentis (*M. epitea* s.l.)	II,III
Salix triandra	***Melampsora amygdalinae***	0–III
Salix triandra [s.l.]	*Melampsora laricis-epitea* (*M. epitea* s.l.)	II,III
Salix triandra × *viminalis*	*Melampsora amygdalinae*	0–III
Salix viminalis	*Melampsora abietis-caprearum* (*M. epitea* s.l.)	II,([III])
	Melampsora farinosa	II,III
	Melampsora laricis-epitea (*M. epitea* s.l.)	II,III
	Melampsora ribis-viminalis	II,III
Salix viminalis?	*Melampsora ribis-epitea* (*M. epitea* s.l.)	II,(III)
	Melampsora ribis-purpureae (*M. epitea* s.l.)	II,III
Salix waldsteiniana (*S. arbuscula* agg.)	***Melampsora laricis-epitea*** (*M. epitea* s.l.)	II,III
	Melampsora ribis-epitea (*M. epitea* s.l.)	II,(III)

Host taxon	Rust taxon	Sori and spores
Salix waldsteiniana? (*S. arbuscula* agg.)	(*Melampsora farinosa*)	II,(III)
Sanguisorba minor	***Phragmidium sanguisorbae***	0–III
Sanguisorba minor* subsp. *balearica (subsp. *polygama*)	***Phragmidium sanguisorbae***	0–III
Sanguisorba officinalis	*Phragmidium sanguisorbae*	0–III
	Xenodochus carbonarius	0?,I,III
Saxifraga adscendens	*Melampsora arctica* (*M. epitea* s.l.)	0,I
Saxifraga aizoides	***Melampsora reticulatae*** (*M. epitea* s.l.)	0,I
	Melampsora sp. (37)	0–III
Saxifraga aizoides?	*Melampsora arctica* (*M. epitea* s.l.)	0,I
Saxifraga androsacea	***Melampsora arctica*** (*M. epitea* s.l.)	0,I
Saxifraga biflora* × *oppositifolia	***Melampsora arctica*** (*M. epitea* s.l.)	0,I
Saxifraga blepharophylla	***Melampsora arctica*** (*M. epitea* s.l.)	0,I
Saxifraga cernua	*Melampsora* sp. (39) (*Caeoma cernuae*)	0,I
	Melampsora arctica (*M. epitea* s.l.)	0,I
Saxifraga exarata	***Melampsora arctica*** (*M. epitea* s.l.)	0,I
	Melampsora reticulatae (*M. epitea* s.l.)	0,I
Saxifraga granulata	***Melampsora vernalis***	0,I,III
Saxifraga moschata	*Melampsora arctica* (*M. epitea* s.l.)	0,I
	Melampsora reticulatae (*M. epitea* s.l.)	0,I
***Saxifraga moschata*?**	***Melampsora epitea*** s.l.	0,I
Saxifraga muscoides	*Melampsora reticulatae* (*M. epitea* s.l.)	0,I
Saxifraga muscoides?	*Melampsora epitea* s.l.	0,I
Saxifraga oppositifolia	***Melampsora arctica*** (*M. epitea* s.l.)	0,I
Scilla bifolia	*Melampsora* sp. (42) (*Caeoma scillae*)	0,I
Senecio alpinus (S. *cordatus*)	***Coleosporium senecionis***	Ib,III*
Senecio cruentus → *Pericallis cruenta*		
Senecio doria	*Coleosporium senecionis*	Ib,III*
Senecio doria agg.	***Coleosporium senecionis***	Ib,III*
Senecio doronicum	*Coleosporium senecionis*	Ib,III*
Senecio erucifolius	*Coleosporium senecionis*	Ib,III*
Senecio germanicus → *S. nemorensis* agg.		
Senecio hercynicus	***Coleosporium senecionis***	Ib,III*
Senecio jacobaea	***Coleosporium senecionis***	Ib,III*
Senecio nemorensis agg.	***Coleosporium senecionis***	Ib,III*
Senecio ovatus (*S. fuchsii*, *S. nemorensis* agg.)	***Coleosporium senecionis***	Ib,III*
Senecio ovirensis → *Tephroseris longifolia*		
Senecio paludosus	*Coleosporium senecionis*	Ib,III*
Senecio rupestris	***Coleosporium senecionis***	Ib,III*
Senecio sarracenicus (*S. fluviatilis*)	***Coleosporium senecionis***	Ib,III*
Senecio subalpinus	***Coleosporium senecionis***	Ib,III*
Senecio sylvaticus	***Coleosporium senecionis***	Ib,III*
Senecio umbrosus (*S. doria* agg.)	***Coleosporium senecionis***	Ib,III*
Senecio vernalis	*Coleosporium senecionis*	Ib,III*
Senecio viscosus	***Coleosporium senecionis***	Ib,III*
Senecio vulgaris	***Coleosporium senecionis***	Ib,III*
Sherardia arvensis	*Pucciniastrum guttatum*	II,III
Solidago gigantea	***Coleosporium solidaginis***	II,(III*)
Sonchus arvensis	***Coleosporium sonchi***	Ib,III*
Sonchus arvensis* subsp. *uliginosus	***Coleosporium sonchi***	Ib,III*
Sonchus asper	***Coleosporium sonchi***	Ib,III*
Sonchus oleraceus	***Coleosporium sonchi***	Ib,III*
Sonchus palustris	*Coleosporium sonchi*	Ib,III*
Sorbus aria	***Gymnosporangium tremelloides***	0,I
	Ochropsora anemones	II,III*
Sorbus aria?	*Gymnosporangium clavariiforme*	0,[I]
Sorbus aucuparia	***Gymnosporangium confusum* s.str.**	0,I
	***Gymnosporangium cornutum* s.str.**	0,I
	Gymnosporangium tremelloides	0,I
	Ochropsora anemones	II,III*
***Sorbus aucuparia*?**	***Gymnosporangium clavariiforme***	0,[I]

Host taxon	Rust taxon	Sori and spores
Sorbus chamaemespilus	*Gymnosporangium cornutum* s.str.	0,I
	Gymnosporangium tremelloides	0,I
Sorbus domestica	*Gymnosporangium cornutum* s.str.	0,I
Sorbus hybrida (*S. aria* agg. × *aucuparia*)	*Gymnosporangium cornutum* s.str.	0,I
	Gymnosporangium tremelloides	0,I
Sorbus intermedia (*S. aria* s.l. × *aucuparia* × *torminalis*)	*Gymnosporangium cornutum* s.str.	0,I
	Ochropsora anemones	II,III*
Sorbus latifolia	*Gymnosporangium clavariiforme*	0,[I]
	Gymnosporangium confusum s.str.	0,I
	Gymnosporangium cornutum s.str.	0,I
	Gymnosporangium torminali-juniperini	0,I
	Gymnosporangium tremelloides	0,I
	Ochropsora anemones	II,III*
Sorbus mougeotii	*Gymnosporangium cornutum* s.str.	0,I
Sorbus torminalis	*Gymnosporangium clavariiforme*	0,[I]
	Gymnosporangium cornutum s.str.	0
	Gymnosporangium confusum s.str.	0,I
	Gymnosporangium torminali-juniperini	0,I
	Gymnosporangium tremelloides	0,I
	Ochropsora anemones	II,III*
Stellaria alsine	*Melampsorella elatina*	II,III
Stellaria aquatica (*Myosoton aquaticum*)	***Melampsorella elatina***	II,III
Stellaria graminea	***Melampsorella elatina***	II,III
Stellaria holostea → *Rabelera h.*		
Stellaria media	*Melampsorella elatina*	II,III
Stellaria nemorum	***Melampsorella elatina***	II,III
Stellaria palustris	*Melampsorella elatina*	II,III
Struthiopteris spicant (*Blechnum s.*)	***Milesina blechni***	II,III
Symphyotrichum lanceolatum	***Coleosporium montanum***	Ib,III*
Symphyotrichum novae-angliae	***Coleosporium montanum***	Ib
Symphytum officinale	***Pucciniastrum symphyti***	II,III
Symphytum tuberosum	***Pucciniastrum symphyti***	II,III
Symphytum ×uplandicum	*Pucciniastrum symphyti*	II,III
Telekia speciosa	***Coleosporium telekiae***	Ib,III*
Tephroseris longifolia (*Senecio ovirensis*)	***Coleosporium senecionis***	Ib,III*
Thalictrum aquilegiifolium	*Tranzschelia thalictri*	III
Thalictrum flavum	*Tranzschelia thalictri*	III
Thalictrum foetidum	*Tranzschelia thalictri*	III
Thalictrum minus [s.l.]	***Tranzschelia thalictri***	III
Thalictrum morisonii	*Tranzschelia thalictri*	III
Thalictrum simplex [s.l.]	*Tranzschelia thalictri*	III
Thelypteris phegopteris → *Phegopteris connectilis*		
***Tropaeolum* sp.**	*Coleosporium tussilaginis* s.l.	Ib,III*
	Cronartium flaccidum	II,III
Tsuga sp.	*Naohidemyces vaccinii*	0,IIa
Tussilago farfara	***Coleosporium tussilaginis* s.str.**	Ib,III*
Vaccinium myrtillus	*Calyptospora columnaris*	III
	Naohidemyces vaccinii	IIb,III
Vaccinium oxycoccos [agg.] (incl. *V. microcarpum*)	*Naohidemyces vaccinii*	IIb,III
Vaccinium uliginosum [agg.] (incl. *V. gaultherioides*)	***Naohidemyces vaccinii***	IIb,III
Vaccinium vitis-idaea	***Calyptospora columnaris***	III
	Naohidemyces vaccinii	IIb,III
Vincetoxicum hirundinaria	***Cronartium flaccidum***	II,III
Viola biflora	***Uredo alpestris***	II
Viola palustris	*Melampsora lapponum* (*M. epitea* s.l.)	0?,I
Woodsia pulchella	*Hyalopsora polypodii*	II,II*,(III)

Appendix 2

Alphabetical list of rust taxa

The present list covers the taxa treated in the main part of this work (those in the introductory chapters are omitted). Selected synonyms are given in parentheses, excluding most names of formae speciales (f.sp.). Selected taxa in square brackets are mentioned under another name but not treated in detail.

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